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ON THE DYNAMICS OF EXPLOITED FISH POPULATIONS

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Series II *Volume* XIX

On the Dynamics of Exploited Fish Populations

R. J. H. BEVERTON, M.A.
and
S. J. HOLT, B.Sc.

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PREFACE

Since the International Fisheries Exhibition in 1883, people connected with the fishing industry have been aware that the yield that can be taken year after year must in some way depend upon natural processes such as growth, mortality and reproduction. Science has sought to estimate the importance of each of these, and to understand their combined effect. Up to the time of the Overfishing Conference in 1946 estimates could be made only roughly and not completely. However, the main need for the stocks of fish in waters adjacent to the British Isles had been shown by experience: namely, to allow them to grow to a reasonable size before being caught.

In 1947, the Standing Advisory Committee, set up by the Convention of 1946, found that it needed more precise information on past changes in the stocks of fish, and more certain predictions of what effects there would be from one measure of conservation or another. The time was evidently ripe for a thorough analytical treatment of the subject, sufficiently good to make use of all existing information. It became necessary to predict the effects of changes in the amount of fishing, in mesh of nets, of variations in growth rate due to thinning out the stocks by fishing and of variations in the rates of reproduction and survival: in general, to determine what effects are of a major order and what minor, and to estimate, for the industry and for governments, the magnitude of the benefits that can be achieved by conservative fishing.

It was always evident that the task set to the authors of this book would be considerable. To consider all the factors in one comprehensive equation demands considerable patience. The number of factors that govern yield, and the variety of fishing, requires the use of a good many algebraic terms. Nevertheless, it will be found that the theory used is relatively simple, and once the notation is mastered this is not a difficult paper to read, especially with its generous provision of simple graphs, and ample worked examples.

Although it will be found that the paper is directly relevant to the better use of the stocks of fish in the North Sea, it is not offered on so narrow a basis, but as a guide in conservation problems over a larger field. Plainly the first application will be in fisheries, but it is hoped that the methods and ideas will also find applications in the study of other natural resources.

MICHAEL GRAHAM

FISHERIES LABORATORY
LOWESTOFT

June 30, 1954

AUTHORS' NOTE AND ACKNOWLEDGEMENTS

The investigations described in this report were carried out between 1947 and 1953. The first statement of the simple equation for steady yield was by H. R. Hulme in 1946 (Hulme, Beverton and Holt, 1947), during correspondence with Michael Graham; it was also deduced independently by P. H. Thomas in 1946 following discussions with the authors. The next stage in our investigations formed the subject of papers read by the authors at a meeting of the Challenger Society at Lowestoft in 1948. These, of which only brief summaries were published (Beverton, 1949; Holt, 1949a), described the simple models as they appear in Part I of the present paper, including the incorporation of von Bertalanffy's growth equation, and also gave an account of their application to North Sea plaice and the use of yield-isopleth diagrams (§17.4). Various references to the progress of the investigations include those of Graham (1951a, 1952), Westenberg (1948) and Beverton (1952). The last named author read a paper at the 1952 meeting in Copenhagen of the International Council for the Exploration of the Sea, which presented those conclusions of the present paper (see §§19 and 20) having a direct bearing on the principles of fishery regulation (Beverton, 1953). Some of the material was delivered in lecture form by the same author at the U.S. Fishery Laboratory, Beaufort, N. Carolina, in 1951, which has since been published as a limited edition by the Beaufort Laboratory (see Beverton, 1954). We are glad to acknowledge here the value to us of discussions with our American colleagues, both then and during S. J. Holt's visit to the U.S. in 1949.

Owing to a lapse of three years between the submission of the manuscript of this paper for printing and its publication, it has unfortunately been impossible to deal adequately with the many important papers on fish population dynamics which have appeared since 1954. Brief reference to a few of the most relevant have, however, been inserted where possible at proof stage, either in the text or in foot-notes.

The authors regret that for reasons of service etiquette their great debts to colleagues at Lowestoft throughout the preparation of this report cannot be acknowledged individually. We are permitted, however, to express our thanks to the Nature Conservancy for their co-operation,* to Dr. J. Westenberg for his continued interest in our work, and to Dr. David Lack, F.R.S., for a critical reading of the manuscript. We wish especially to acknowledge our appreciation of discussions and exchange of ideas with Mr. B. B. Parrish and Mr. R. Jones of the Marine Laboratory, Aberdeen, who also gave a critical reading to parts of the manuscript and provided us with some unpublished data. These workers have recently published an application of theoretical models, similar to those developed in this paper, to the Faroe and North Sea haddock fisheries (Parrish and Jones, 1953), adopting for the reader's convenience the same symbols for the main parameters as we have used. Although this publication is too recent for us to make detailed reference in the text, it may be noted here that their conclusions for the North Sea haddock are broadly similar to our own. Finally, we wish to express our thanks to Dr. G. L. Kesteven of the Fisheries Division of F.A.O., who has honoured us by regarding his kind assistance in preparing the index as a contribution to his own studies on the concepts and terminology of fisheries science.

R.J.H.B.
S.J.H.

June 30, 1954

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* S. J. Holt was a member of the staff of the Fisheries Laboratory, Lowestoft, from 1946 to 1950, during which time the greater part of the investigations described in this report were carried out. He then joined the Nature Conservancy, who kindly permitted him to assist in the preparation of the manuscript. Holt is now on the staff of the Food and Agriculture Organisation of the United Nations, Rome.

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PART I

Fundamentals of the Theory of Fishing, illustrated by Analysis of a Trawl Fishery

> "*. . . one of the commonest methods of operational research involves the setting up of one or more possible imaginary models, studying their expected characteristics and seeing which fits the data best*".
>
> SIR CHARLES GOODEVE IN *Nature* 1948

SECTION 1: INTRODUCTION

THEORETICAL METHODS IN THE STUDY OF FISHERY DYNAMICS

The investigations described in this report were started at the beginning of 1947 as part of the post-war programme of research into the dynamics of the populations forming the natural resource on which depend the demersal fisheries of the North Sea. By that time it was already clear (see Graham, 1951b, Fig. 5) that these stocks which had, as was expected, increased enormously because of the cessation of fishing during the war, were declining rapidly. Calculation of the survival rate of North Sea plaice in 1946-7 (Holt, 1949b) showed that this was at least as low as during the years 1937-9, and it was evident that the final catch per trip was going to be considerably lower yet; which fear, expressed by Beverton (1948) in a contribution to a conference on British Food Needs and Resources held in 1947, has subsequently been justified.

The International Overfishing Conference held in 1946* reaffirmed the desire of all nations fishing the North Sea to regulate their fisheries in some way, and the main purpose of this paper is to provide a basis for scientific advice as to the way in which these desires may be translated into action. The paper is necessarily long, because it was essential at this stage that a theoretical structure which was above all comprehensive should be developed, but the authors hope that any difficulties that the reader may have in following a particular line of reasoning will be minimised by the provision of a full contents list and a resumé, and the extensive use of cross-references.

We make no apology for the fact that much of what is to follow is mathematical in nature. It is now generally accepted by fishery naturalists, and in fact by most workers dealing with population problems, that mathematics is an indispensable tool in their studies. If any defence of its use in biology or economics is still required, this has been most convincingly provided by W. R. Thomson (1939), Kostitzin (1939) and more recently by von Neumann and Morgenstern (1947). Our method has little in common with that of Petard (1938), and in effect has been essentially that advocated by Rafferty (1950), namely to construct simple algebraic models of fish populations, to study their reaction to varying types and intensities of exploitation and to elaborate them where the available information showed that this was necessary. Well known standard statistical methods have been used in interpretation and treatment of the basic data; beyond that little more is asked of the reader than an acquaintance with the elementary techniques of the differential calculus.

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*See *Final Report of the Standing Advisory Committee to the International Overfishing Conference*. H.M.S.O., London, 1948.

In a sense the population models we have used were old-fashioned before they were developed, since they are in nearly all cases 'deterministic'. This means, in effect, that the factors responsible for the dynamics of a population are assigned constant numerical values; hence, as Moran (1950) has put it, " . . . once the constants and the initial values of the population densities are given the development of the situation is determinate". During the last decade, models have been developed in which probability theory is used to determine their functional relationships. In these 'probabilistic' models account is taken of the fact that, in reality, population parameters do not have constant numerical values but fluctuate to a greater or lesser extent under the influence of chance events. Considering population change as a stochastic process, in this way, often gives results appreciably different from those obtained with deterministic models (see Bailey, 1950; Bartlett, 1949; and D. G. Kendall 1949), especially for the prediction of critical phenomena such as total extinction of the group. It is our belief, however, that, except in particular instances which have been indicated in the text (e.g. in §6, dealing with the egg-recruit relationship), the multiplication of effort both in deriving the stochastic equations and in computing them would not have been justified when the standard of accuracy of our data, the complexity of the biotic system with which we are dealing, and the order of magnitude of the expected discrepancies, are all taken into account.

Similar conclusions as to the continued practical use of deterministic models in a related field—the experimental study of the dynamics of populations in cultures—have been reached by F. E. Smith (1952), who has pointed out that although it is only stochastic theory that "permits evaluation of an actual, observed curve, regardless of its irregularities", such comparisons of whole theories with, in this case, culture growth curves, may not be the best way to test the theories. Apart from the importance of deterministic thinking as a way of producing new concepts—since "inevitably one considers, not the sequential range of values, but the most likely course of events"—this author pleads also for the rigorous testing of separate aspects of deterministic theories, not only to simplify the mathematics, but to decrease the prior probability of obtaining a 'good fit'. It would appear to be doubly important to find and use such critical methods in field studies, where one has little if any control over the environment. Indeed Graham (1951 (a), Fig. 8) has demonstrated the paucity of data relating sustained yield to fishing effort for a number of important marine fisheries.

Southern (1948) has remarked that " . . . the blunders which man has made in the field of biological control can only be eliminated by a shift from hasty empirical methods to an attack on first principles", and like him, we have placed much emphasis on the fundamental study of populations in steady state. Although our object has been primarily a practical one, we have as our subject what is really a special case of the general problem of predation and interaction between populations, a fact recognized by Thomas Park in his survey of selected population problems (Allee, Emerson, Park, Park and Schmitt, 1949, pps. 377-379. See also Walford 1947, p. 385). It has accordingly been necessary to digress in some sections and, drawing on data from widely scattered sources, to examine rather more deeply the factors governing what Huntsman (1948) has termed the *biapocrisis* of the organisms as a whole, that is, the reaction of the individual to its environment by reproducing, growing, moving and surviving; and finally, to incorporate our findings in theoretical models of the population. Much of our investigation has taken this form—a widening of our front followed by a narrowing of it again but with more light thrown on the problem in question, and we hope that what we think is a new approach to the questions of density dependence, competition and dispersal, will prove useful in fields other than that with which we are directly concerned.* For similar reasons the bibliography is large, although only those papers to which specific reference is made in the text are included. It is thus reasonably comprehensive, but must not be regarded as an attempt to provide a complete list of the relevant literature. We have, however, endeavoured to mention all the important, and the majority of less important documents dealing with fisheries control and management.

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*A case in point is our belief that ecological field work on populations must be more closely linked than is usual with those branches of biology dealing with individual organisms. This applies particularly to physiological and behaviour studies, for without these satisfactory population models cannot be formulated. Instances are investigations of metabolism in connection with the density-dependence of growth (§9.4.3); of animal orientation as related to models of fish movement and spatial variation of factors (§10.2.5); and of food preferences and selective grazing (§§9.4.3.2.3-5). In these and other cases new developments of the specialised fields can be foreseen in which experimentation in the laboratory is much more directly related to ecological problems.

Until 1942, when E. S. Russell published the lectures on 'Overfishing' which he had delivered at Baltimore immediately before the war, two main, though by no means independent, theoretical lines of approach to that problem were distinguishable. The first, originating in Baranov's 1918 paper and contributed to principally by E. S. Russell (1931 and 1939) and Thompson and Bell (1934), considered the vital properties of particular populations separately; the rates of change in weight and numbers were treated as independent constants and integrated in such a way as to allow assessment of the steady states corresponding to different amounts of fishing. M. Graham, on the other hand, although he made in 1935 an application of Russell's equation to the North Sea fisheries, outlined in the same paper what has come to be referred to as the Sigmoid Curve theory. This idea, which is related to Hjort, Jahn and Ottestad's (1933) use of the logistic curve of population growth and their interpretation of its slope at any point as representing the catch which a population of that size could sustain, was elaborated by Graham in 1939 and its implications discussed more fully in 1943. Since then Baerends (1947) and, more especially, Schaefer (1954) have developed the method further and applied it to data of several fisheries. It has also been invoked in discussion of the rational hunting of wild animals other than fish (e.g. Leopold, 1951).

Perhaps because of the lack of data referring to large-scale changes in abundance of fish stocks, but more probably because of the very real difficulties of interpretation underlying the apparent simplicity of the sigmoid curve theory, it is the former, analytical trend to which most attention has been paid since the war. Although recognising that the two approaches are convergent, it is the analytical method that we, too, have used for the most part. Certain of our results have been anticipated whilst the investigation was in progress, and particular mention must be made of Ricker's study of marking theory (1948) and discussion of compensatory mortality (1954); and of Moran's (1950) account of the conditions for self-induced population oscillations. We hope that adequate reference to these and others has been made in the appropriate sections. We do not claim originality in all that is to follow; on the contrary, part of our purpose has been to unify past work and put existing ideas—ideas the development of which can be traced back in a direct line to the great naturalists of the last century, and to Frank Buckland in particular—into a new and, we hope, more satisfactory theoretical framework. One essential aspect of this synthesis is the recognition of a fish population or community of populations as a self-maintaining *open system*, exchanging materials with the environment and usually tending to a steady state. For this appreciation, as well as for the specific work on the growth of individual organisms, we owe a great deal to the writings of L. von Bertalanffy (1938 and 1949), and in a more restricted sense to the rapidly growing literature on the theory of automatic control of machines and industrial processes.

The significance of open systems in biology has been discussed in detail by von Bertalanffy (1950a and b, 1951), who notes the rôle of feed-back in homeostatic processes, making reference to the work of Frank *et al.* (1948). The development of this present paper may be regarded, in von Bertalanffy's terms, as a step in the transition from the view of an exploited fish population as an open system exhibiting physical summativity (i.e. independence, in this context) of the variations of the elements comprising it, to one in which that system—behaving as a unit through the interaction of the primary processes of birth, growth, mortality and movement because of their mutual dependence on age and population density—is itself but one element in a higher system comprising all the other inter-dependent biotic groups, including man and other predators, competing animals, species at other levels in the food chain and so on.* Since by far the most important way at present of exploiting the organic resources of the sea is to catch certain selected species of direct commercial importance as opposed to a deliberate attempt to utilise the productivity of a marine community as a whole—and this will remain so for some time to come—our immediate concern is with the resultant reaction to man's activity which these species show, rather than with changes in the total marine productivity thus brought about.

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*In the above discussion we have referred primarily to von Bertalanffy's views on open system theory because he has presented them in a form that is particularly relevant to our subject. Many other authors have, of course, contributed to the development of this concept; among them Burton (1939), Needham (1943), Hutchinson (1948), Hempel (1951), Bass (1951) and Jonas (1951).

How far it is possible to advance along these lines remains to be seen, but it is reasonably certain that sooner or later a more comprehensive approach will be required. Elton (1949) has suggested that the goal of ecological survey is "... to discover the main dynamic relations *between populations* living on an area" (italics ours). This is a generalisation of what is now perhaps the central problem of fisheries research: the investigation not merely of the reactions of particular populations to fishing, but also of the interactions between them and of the response of each marine community to man's activity. Here the main question is the extent to which it is possible and practicable to derive laws describing the behaviour of the community from those concerning the properties of component populations. Judging by ecological experience it seems fairly certain in such a case that 'the whole will be more than the sum of its parts', and from this point of view the sigmoid curve theory remains the most successful attempt so far to state concisely and in general terms what form the reaction of a community to the exploitation of one or more of its constituent populations might be expected to take. Nevertheless, it is the parts—the vital statistics of particular species—that are measured by present methods, and it is clearly one of the main requirements of mathematical-deductive analysis that it should suggest possible functions which the whole might be of its parts. Indeed, the comparison of community behaviour predicted in this way with observed phenomena may well be a powerful method of distinguishing and understanding the mechanisms that are peculiar to the community level of integration.

Were we writing in 1943, our introduction would necessarily stress the importance of W. F. Thompson's work in the bold and inspiring achievement of regulation of the Pacific Halibut fishery. Writing as we are in 1953 it would be incomplete without mention of his most vigorous critic. We refer to Martin D. Burkenroad's important and provocative contributions (1948, 1950, 1951), and whilst this is not the place to discuss these in detail some evaluation of the last of these publications is called for. Whilst applauding his vigorous attack on some loose and inconclusive thinking about this matter, and agreeing, reservedly, with his conclusion that regulations to conserve marine fisheries must be conceived in such a way that the results can be examined on a sound statistical basis, we nevertheless feel that he has over-emphasized the importance of the inductive method as compared with that of the deductive. This is perhaps because the over-fished species of which we have first-hand knowledge are in fact those for which, as Burkenroad concedes, the accidents of war provided conclusive proof of what he calls significant fishery-dependent changes. The evidence that in these cases the process of depletion is truly reversible is provided by Borley's (1923) report of the effects of the 1914-18 war and numerous papers read at the 1947 Symposium on the effects of the Second Great War, convened by the International Council for the Exploration of the sea.* Yet if other fisheries for which there are no such direct observations show similar symptoms of maladjustment, then surely it is a useful starting hypothesis that there, too, fishing effort is being wasted in merely reducing the stocks to uneconomic levels. This view can be held without departing in any way from the tradition dating from T. H. Huxley's time, and reaffirmed by Graham, that the best management of fishing is to leave it alone until events show that intervention is necessary. Measurements of the observed effects of sustained changes in fishing intensity are very convincing, but even when these are available deductive reasoning is necessary to interpret these effects, to assess the likelihood of their stability and to distinguish them from the fishery-independent changes to which Burkenroad attributes great importance. This latter view has been criticised by Kesteven (1950), who considers that in the past the existence of large natural fluctuations in population abundance has not been overlooked, nor has their importance been underestimated, and he cites Hjort's (1914) work on the Northern

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*See *Cons. Int. Explor. Mer, Rapp. et Proc.-Verb.*, 122, 1948.

European species. This and other similar studies have, however, been concerned usually with irregular year-to-year fluctuations in abundance, and although it is true that these do not in any way weaken the arguments for the existence of an optimum fishing intensity—nor even, as we shall show, affect its magnitude to an appreciable extent (see also Needler, 1948)—nevertheless, in his later papers especially, Burkenroad is concerned rather with longer-term fishery-independent (i.e. 'natural') trends or oscillations. If the possibility of the occurrence of these be admitted, as we think it must be, it is equally true that great caution must be exercised in the interpretation of events during the experimental management phase; but even so, the temporal coincidence of fishery limitation and a sudden change in the stocks *in a favourable direction*—and one, furthermore, which could not have been in any way foreseen by scrutiny of previous statistics—must be regarded, *a priori*, as unlikely (compare for example the experience of trial and error methods in stocking lakes with *Coregonus clupeaformis* Mitchill, described by Miller, 1949).

The fallacy that scientific method is to be identified solely with inductive reasoning has, we think, led Burkenroad to make an unnecessarily rigid division between the tasks of the biologist and of the political economist. Given that each must keep in general to the field within which he is supposedly expert, to restrict the former to 'the prediction of the effects of exploitation upon fish stocks' would prevent his drawing some legitimate conclusions from his studies. For example, although, as we shall show, the simple idea of a single biologically most effective rate of fishing coinciding with an inflexion point in the curve of diminishing return from increasing expenditure of effort, must now be discarded or at least modified, nevertheless there are definite biological statements to be made, the significance of which cannot be appreciated without first an excursion into the economist's domain. Some overlapping is thus highly desirable; and we would go further, in suggesting that the biological requirements cannot be regarded as simply one among many independent factors of which administration must take account.

Burkenroad's interesting suggestion that regulation should take the form of a controlled experiment with periodic relaxation of the restrictions cannot be dismissed lightly but the reservations referred to earlier are important. The administrative difficulties might be great and the economic and social consequences far-reaching, although the potential value of such a system of control, which by the end of a given period would permit accurate assessment of the effects of management, must be given due weight. In the North Sea, with the confidence that knowledge of the effects of two wars has given us, this criterion would almost certainly be satisfied by the *continuous* operation of regulations designed to limit fishing effort or adjust gear selectivity, provided that satisfactory commercial statistics, of the standard outlined by Beverton (1952), were available; that a critical study of the magnitude and age composition of the catches was made; and that checks on the effects of that effort on the growth and mortality of fish were ensured, by marking experiments and other means. It is with this kind of procedure in mind that we have made, in §19.2.3, tentative enquiries into the way in which this information obtained after the imposition of prescriptive regulations might be analysed, and we have concluded that control charts based on the same principles as those used in the quality control of manufacturing processes could, if suitably developed, be a most useful tool for this purpose. F. E. Smith's (1952) comment that "any experimental technique which will produce a steady state should yield information that can be used in deterministic theory" is pertinent here. We have found, repeatedly, that with a knowledge of population statistics for two steady states much unravelling of the dynamic processes is possible and prediction of changes can profitably be attempted.

There can be no reasonable doubt that management costs in the North Sea would be negligible compared with the benefit to the industry and to the community. Whilst agreeing that one important benefit would be an improvement in our knowledge of the interaction between man and his environment, we cannot concur with Burkenroad's belief that the net *material* gains to society would be small; on the contrary, though we do not hold out much hope of a greatly increased demersal yield, the landings could certainly be maintained with far less than the present effort. In this way not only would the demersal catch be made at much reduced cost, but ships and men would be released to intensify exploitation of the stocks of underfished species. As a first step, however, Graham (1951a) has stressed that to remedy the ills of the industry, stabilisation of the fishing intensity is more important in itself than is achieving the optimum. This would still allow advantage to be taken of subsequent technological improvements so long as compensating reductions were made in the total effort.

In a sense the foregoing remarks belong rather to the end of this paper than to the beginning, and yet unless our position were clarified at the outset the necessary pattern of what is to follow might not be fully appreciated. In our work there are gaps, and possibly inconsistencies --both apparent and real—but in his review of the Marine Resources Section discussion, Graham (1950) reminded the delegates to the U.N. conference that "life does not stand still while specialists put their minds in order", and we must uphold the general validity of the conclusions of our predecessors which our studies have done no more than underline and codify.

SECTION 2: THE BASIS OF A THEORETICAL MODEL OF AN EXPLOITED FISH POPULATION AND THE DEFINITION OF THE PRIMARY FACTORS

The basic principles on which depend the dynamics of an exploited fish population were appreciated by several workers before Russell (1931), such as Buckland (see Graham 1948), Petersen (1903) and particularly Baranov (1918). We shall make detailed reference to Baranov's work and that of other authors in §17.8, but Russell's paper gives an exposition of the fundamentals of the problem in the form most convenient to take as a starting point for the development of our theoretical population models.

The axiom taken by Russell is that the weight of a population remains stabilised if, over a given period of time, the weight increments are equal to the weight decrements. This statement is self-evident, but the value of Russell's contribution was that he showed its significance when applied to fishery problems. In so doing he drew attention to certian important points. One of these is the value of considering populations in a steady state. Another is that the axiom is true not only for a complete population, but also for any part of it made up of individuals between any two ages. Finally, Russell stated the primary factors contributing to the balance of weight increments and decrements in any phase, as defined above, of a closed fish population, that is, one in which there is no emigration or immigration. These are:

(a) *Recruitment* of individuals to the exploited phase of the life-cycle,
(b) *Growth* of individuals in the exploited phase,
(c) *Capture* of individuals in the exploited phase by fishing,
(d) *'Natural' death* of individuals in the exploited phase,

i.e. from all causes other than capture by man. The first two of these are responsible for weight increments, the latter two for weight decrements. Strictly speaking, there is need to add to the latter the weight decrements due to the loss from the fished population of individuals which have become older than the upper limit of age defining that phase, but we may ignore this factor for the moment.

Russell denoted the weight increments and decrements due to the four above factors during any specified interval of time by A, G, C and M, respectively, and was then able to express his axiom in the symbolic form:

$$S_2 = S_1 + (A + G) - (M + C) \qquad \text{.. .. .. ..} \qquad (2.1)$$

where S_1 and S_2 represent the total weight of the exploited phase of the population at the beginning and end respectively of the time interval over which the increments and decrements are defined. While (2.1) can lead to certain important conclusions, it is not in a form suitable for analytical purposes, as Russell himself realised. This is because the actual weight increments or decrements are not independent of each other, but (2.1) contains no reference to the way in which they are inter-related. Moreover, from the point of view of practical application, only the weight decrement due to fishing (the yield) can be estimated directly. Russell's equation contains the essentials of a theoretical model of an open system but has the limitation that the factors involved are represented as their integrated effect. For this reason (2.1) is a correct formulation of past events but cannot be used to predict future behaviour.

The key to the problem is the question of the interdependence of the primary factors. In (2.1) this has both direct and indirect components. The direct component has a purely formal basis, and arises from the fact, for example, that the magnitude of the yield, C, depends directly on that of the weight decrement M due to natural causes, and vice-versa, i.e. one and the same fish cannot both be caught and die naturally. The indirect component is due to certain biological properties of the system, and concerns primarily the effect on the magnitude of recruitment, natural mortality and growth (and hence on the yield) of the population density, the magnitude of which is itself the resultant of these factors. The direct component of interdependence of the primary factors can be eliminated by expressing the latter in appropriate mathematical forms; more specifically, this amounts to defining each factor in terms of parameters or coefficients that are themselves independent. This approach provides the basis for the development of the simple population models in Part I of this paper, in which we make the simplifying assumption that the parameters are constants and, in particular, independent of population density. It is important to note that whereas direct interdependence is rigorously eliminated in this way, the validity of the population model depends, *inter alia*, on whether the effects of indirect interdependence are small enough to be ignored. Often this will not be the case, and in Part II we introduce indirect interdependence into the simple models—a problem which has not previously been approached in this way. Thus the theoretical models of Baranov (1918) and Ricker (1940, 1944) eliminate the direct component of interdependence only. The method adopted by Graham (1935), on the other hand, takes account implicitly of both kinds of interdependence in that his model represents the resultant effect of all factors and their interaction, but does not lead to an analytical population model of the type we are considering (see §17.8).

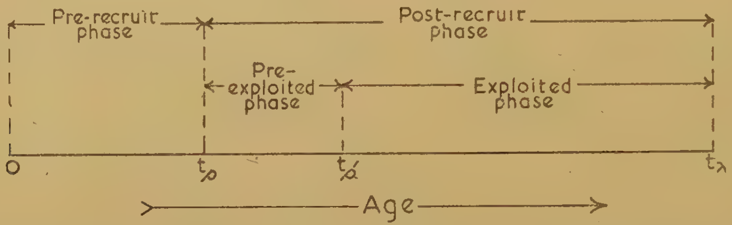
In addition to the four primary factors listed above which form the basis of the simple models, there is a further one which must be mentioned at this stage, namely the movement or dispersion of fish within the fishing area. The problems involved in the study and mathematical representation of this factor are complex, and since it is not essential to the simple models it is considered separately in §10.

SECTION 3: MATHEMATICAL REPRESENTATION OF THE FOUR PRIMARY FACTORS

In this section we review briefly the range of characteristics of the four primary factors defined in the previous section that are likely to be met with in the demersal fisheries of Northern Europe, with special reference to those for plaice (*Pleuronectes platessa* L.) and haddock (*Gadus aeglefinus* L.). In each case we specify here the simplest mathematical form that gives a reasonable representation of the factor in question in terms of parameters which can, in the first instance, be assumed to be constant and independent, and indicate the later section (in Part II) where a more detailed treatment is given.

3.1 RECRUITMENT

We shall define the *age at recruitment*, t_ρ, as the age at which fish enter the area where fishing is in progress, that is, at which they become liable to 'encounters' with the gear, as defined in §3.3. The number of fish from each brood which reach this age we denote by R, and thereafter regard them as part of the *post-recruit phase* of the population. In some species there may be little marked geographical segregation of the young stages from the adult population, in which case recruitment would correspond to the adoption of a benthic habit. In other species, of which the North Sea plaice is a good example, the young, or *pre-recruit*, fish occupy nursery grounds where adults are not present in appreciable numbers. In these cases, recruitment to the main exploited area is by means of a migration from the nursery grounds. Whether or not newly recruited fish are retained by the fishing gear in use depends on its selective properties and the size of the fish. In general, fish will first become liable to capture, and hence enter the *exploited phase* of the population, at some later age, $t_{\rho'}$. The number of fish of a given brood surviving to this age we denote by R'. The above definitions can be illustrated diagrammatically as follows:—



It should be mentioned at this point that previous population models have referred only to the exploited phase of the population, and the term recruitment has been used for the entry of young fish to this phase. To analyse the effects of varying the selectivity of the gear (see §3.3) and certain other more complex phenomena, it is essential to consider the whole of the phase during which fish are exposed to encounters with the gear. For this reason we use the term recruitment in the biologically more fundamental sense of denoting entry of fish to the exploited area, but it should be remembered that for certain special purposes the former definition may be more apt. Thus in marking theory it is the number of animals liable to be caught by the trapping system in use that is important, and Leslie (1952) has used the term *dilution* to refer to immigrants, births, or young that have grown up to enter the population at risk of capture.

Studies on the life history of many demersal fish have shown that a very high mortality of young occurs prior to adoption of a bottom habit (and hence before recruitment) and mostly within a short time of the eggs being laid. This mortality, and thus the number of recruits, R, is greatly influenced by environmental conditions. The number surviving from a given brood of eggs depends also on the number of those eggs and hence on the abundance and other characteristics of the adult population which spawned them, though evidence from a number of species suggests that this latter relationship is likely to be detectable only when the population density varies over a very wide range. Treatment of the relationship between the number of recruits and the size of mature population from which they originated, and of fluctuations in the annual number of recruits, is given in §§6.1 and 6.2, respectively. For the simple population model we assume that a constant number of fish are recruited on the same date each year.

3.2 NATURAL MORTALITY

A distinction may be made between a natural mortality due largely to a single factor, such as a major predator, and that which is the effect of a relatively large number of environmental factors acting independently. The former type can be dealt with adequately only by taking specific account of the casual factor, and the case of predation is included in a discussion of community dynamics in §11. The latter type is probably more usual among North Sea demersal populations and it will be this to which we refer when using the term 'natural mortality' in this paper (see §7.1). The rate of natural mortality at any time t, which we shall denote by $_M(dN/dt)$, depends on the number of fish present at that time, and in the simplest case we may write

$$_M\left(\frac{dN}{dt}\right) = -MN \qquad \ldots \quad \ldots \quad \ldots \qquad (3.1)$$

This is the form used by several authors, including Baranov (1918), Graham (1935), Schaefer (1943) and Ricker (1944), and although suitable as a first approximation it is necessary to remember that there are few published data that can support it in detail. It may usually be taken to imply that natural death is due to a large number of causes acting randomly, and that the probability of a particular fish dying between any time t and time $t + \Delta t$, is constant. More precisely, we may expect the natural mortality coefficient to vary with age of fish, the theoretical consequences of which are discussed in §7.2.1, and also to be dependent on population density (§7.3). For the simple population model, however, we shall assume that the natural mortality rate can be represented by (3.1) above, the coefficient M being constant and effective from age t_ρ onwards.

A problem which may conveniently be mentioned in connection with natural mortality concerns the *life-span*. If the natural mortality rate remains constant the maximum life-span will, hypothetically, be of infinite duration, though in practice, if we consider any one finite brood of fish, there will come a time when the last survivor dies. Previous authors who have dealt theoretically with the life-span (e.g. Baranov and Ricker) have in fact assumed it to be unlimited, but this can give rise to serious discrepancies if combined, as in the treatment of these authors, with certain assumptions concerning the behaviour of other factors, such as growth, with increasing age (see §17.8). For constructing a population model we suggest that a better procedure may be to terminate the life abruptly at a certain high age which we shall denote by t_λ, so that all surviving fish die at this age. The value of t_λ, in any particular case, will be largely arbitrary; in practice it will be chosen to correspond with the greatest age for which adequate data are available, since data will inevitably become progressively less for fish of increasing age. A further discussion is given in §7.2.2.

3.3 Fishing Mortality

The correct mathematical formulation of fishing mortality and its dependence on the characteristics of both the population and the fishing activity is clearly of great importance in developing a theoretical model of a fishery. A detailed discussion of this problem is given in §8.3.1; here it will be sufficient to state certain general principles and relationships.

A preliminary definition of terms is required at this stage. We use the term *fishing power* to denote the catching power of an individual vessel, and this is measured as the ratio of the quantity caught by that vessel per unit fishing time to that by a vessel selected as a standard reference, fishing at the same time and place and using a standard gear, i.e. both vessels being taken as fishing on the same density of fish (see §12). In this way each vessel of a fleet can be allocated a *power factor* (P.F.), and the fishing time of each vessel can be reduced to standard units of effort by multiplying by its power factor. The *fishing effort* of a fleet we then define in the units 'total standard hrs. fishing/year', and *fishing intensity* as the fishing effort per unit area in the units 'total standard hrs. fishing/year/square nautical mile'. The terms 'fishing effort' and 'fishing intensity' are often used synonymously in fishery research, but we are here distinguishing them in accordance with the use of the words 'effort' and 'intensity' in physical sciences, and the terms are not interchangeable. It should be noted also that 'fishing time' cannot be used in place of 'effort' unless the fishing powers of the vessels (and their gear) concerned remain constant. Thus while 'catch per unit effort' can be used in many instances as a reliable index of density, 'catch per day's absence or catch per 100 hrs. fishing' cannot unless the above criterion is satisfied.

For the simple population models we regard it as a necessary characteristic of demersal fishing activity that there is a random element in the relative movement of fish and gear.

By this we do not mean that fishing is to be regarded as haphazard, but that the relative distribution of vessels and fish at any moment is not determined mainly by their ability to 'sense' each other. The probability of any one fish encountering a unit of gear in a given period then depends on the *fishing intensity* as defined above. Hence the frequency of encounters between fish and gear will be proportional to the product of the fishing intensity and the density of fish; furthermore, a certain fraction of these encounters will result in capture. For the simple case we can assume that the chance of encounter and subsequent capture for a given fish is unaffected by it having experienced previous encounters. We can then define the instantaneous rate of decrease in numbers of the population due to fishing as

$$ {}_F\left(\frac{dN}{dt}\right) = -FN \quad .. \quad .. \quad .. \quad .. \quad (3.2) $$

The *fishing mortality coefficient*, F, can now be seen to be directly proportional to the fishing intensity, f, and we have the relationship

$$ F = cf \quad .. \quad .. \quad .. \quad .. \quad .. \quad (3.3) $$

where c is a constant. It is important to note that F is proportional to the concentration of fishing in space. If the total exploited area can be taken as constant in size and if fishing is distributed either uniformly over it or in a constant way relative to the fish concentrations, then F is also proportional (though by a different constant) to the *fishing effort*, but the departures from this simple situation are of great practical importance (see §§8.3 and 10.2.3). A further point of interest concerning the interpretation of (3.2) is the relationship between F and the probability of capture, p_t, between times t and $t + \Delta t$, which is that

$$ \frac{p_t}{\Delta t} \rightarrow F $$

as

$$ \Delta t \rightarrow 0 $$

a similar relationship holding for M of (3.1) and for the total mortality coefficient $(F + M)$.

The differential equation (3.2) has been generally employed for representing the fishing mortality, for example by Baranov, Graham, Ricker, Schaefer (1943) and Silliman (1945). It has a solution which predicts that the number of fish comprising a year-class will decrease exponentially with age as the result of fishing*, and a closely exponential trend has been found in a number of fisheries, both demersal and pelagic, including the North Sea plaice and haddock (see §13 and Jensen, 1939). This gives strong support to the validity of (3.2) though it is not a complete proof unless natural mortality is either negligibly small or itself adequately represented by a constant instantaneous coefficient, as in (3.1), and these requirements have seldom been established directly.

We must next consider the variation of F, or in effect, the change in the probability of capture, with age. This occurs either if the frequency of encounters with gear, or the likelihood of capture following an encounter, is different for fish of different ages. We have already defined t_ρ as the age at which fish become liable to encounters with gear, and $t_{\rho'}$ as the age at which the probability of capture becomes finite. It is known, however, that the selective action of nets does not cause all individuals to have the maximum probability of capture on reaching a certain critical size, but that the probability of being caught by gear of given selective properties varies over a certain range of size of fish, which is termed the *selection range*. A detailed treatment of the effect of gear selectivity on the variation of F with age is given in §8.1.1. Here we make the simplifying assumption that the probability of capture for all fish of a given year-class remains zero until an age $t_{\rho'}$ is reached corresponding to the 50% point of the selection ogive, at which the probability of capture, and hence the fishing mortality F, takes its maximum value. We refer to this as *knife-edge*

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*Another method of deriving this exponential relationship is given by Morse and Kimball (1951).

selection, and it may be regarded as the limiting case of a selection ogive as its spread or dispersion tends to zero. In addition to the mechanically selective action of gear, there is the possibility with trawls or seines that F may vary with age owing to the greater ability of older fish to avoid capture by swimming out of or away from the mouth of the net (Hickling, 1935). Some evidence was obtained from recent gear experiments on plaice which suggests that this might happen (§14.2.1), and the phenomenon is treated theoretically in §8.1.2.

A further problem is that of assessing the effects of sudden changes or trends in the magnitude of the fishing mortality coefficient. In these circumstances the population will not be in a steady state, and different methods are required to set up the appropriate theoretical models (§8.2). An important practical use of such models is the assessment of changes during the transitional phase following the introduction of a regulative measure involving a change in fishing intensity or in the selective properties of the gear.

Finally, there are the problems raised by spatial variation in fishing intensity within the exploited area (§10). These include the relationship between fishing intensity and the fishing mortality coefficient which, for the area as a whole, is no longer one of simple proportionality in this case; and the reaction to exploitation of a population of which part only is fished at any moment although there is interchange of fish between this part and the rest of the population.

For the simple models we assume that the fishing mortality coefficient is constant for fish between age $t_{\rho'}$ and the end of the life-span, t_λ, and that the fishing effort is distributed uniformly over the population and is maintained at a constant level over a period of years long enough for the population to have reached a steady state.

3.4 GROWTH

Growth in weight of individual fish is usually the most easily measured and best known of the primary factors, and can adequately be described by a sigmoid curve approaching an upper asymptote with increasing age. The curve is markedly asymmetrical, with the inflexion occurring at a weight well below half the asymptotic weight. Superimposed on the sigmoid pattern there may be seasonal variations in the rate of growth; in North Sea plaice, for example, growth virtually ceases during the winter months. For the present purposes, however, we need deal only with the general sigmoid pattern of growth, and for the simple models we must regard this as unchanging*. To this extent our immediate requirement is for a mathematical function to which we need attach no greater significance than that it should give an adequate fit to data of weight-at-age (see, however, §9.1).

Relatively few authors concerned with the theoretical treatment of the dynamics of fish populations have considered this aspect of the problem in much detail. Baranov (1918), for example, has taken a proportional increase in length with age; Hulme, Beverton and Holt (1947) have used a linear increase of weight with age; while Ricker (1944) assumes that this increase is exponential. None of these relationships gives rise to a sigmoid growth curve, though each may fairly adequately describe certain phases of the growth pattern over a limited range of age. Yoshihara (1951) has modified Baranov's treatment by incorporating a logistic equation for growth in length; but this implies that the latter follows a symmetrical sigmoid curve, which is not the case (see also §17.8). It is of course possible to obtain a purely empirical representation of any set of data by means of a polynomial expression, though to obtain in practice the characteristic S-shaped growth curve with this kind of function results in a population model which is rather cumbersome. A more serious disadvantage of this or any other empirical growth function—by which we mean one not based on an analysis of the fundamental processes involved—is that the coefficients it contains have no physiological significance, and there is therefore no means of knowing how they might be expected to change as the result, for example, of variations in food supply or other environmental factors. This does not matter as far as the simple population models are concerned, but it completely precludes the possibility of taking account of important relationships such as the variation of growth with population density, and hence of eliminating the indirect component of factorial interdependence in the simple models. The question is therefore whether a function can be found that not only gives a good and conveniently simple representation of data, but that can also be used for analytical studies of growth phenomena.

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*This concept of 'constant growth pattern' is referred to frequently in this paper. Strictly, we mean that the mathematical function describing the change of weight with age contains parameters whose numerical values are constant. We do not mean that the rate of growth, i.e. dw/dt, is constant, which would imply a linear change of weight with age.

There has been a number of attempts to define generally the physiological processes responsible for the observed pattern of growth of animals, and to give them a mathematical formulation, the more relevant of which are surveyed in §9.1. The value of such attempts has been doubted by Medawar (1945) who remarked, truly, that "the universal growth equation is......a fiction". The important question is not, however, whether a universal representation of growth in a mathematical form is possible, but whether a representation can be made that is adequate for a particular purpose, and in our opinion a function has been developed that satisfies the essential requirements of the present problem. This is the one developed by L. von Bertalanffy (1934, 1938, 1949)*, and in view of the considerable use we make of his growth equation it is necessary at this stage to give a brief account of the underlying concepts and mathematical derivations.

Following earlier students of growth, von Bertalanffy regards an organism as analogous to a reacting chemical system obeying the law of mass action, and groups the physiological processes responsible for the mass of an organism at any time into those of catabolism (breakdown) and of anabolism (synthesis). He then expresses the rate of change of weight of an organism, dw/dt, in terms of some powers, n and m, of the body weight w by the equation

$$\frac{dw}{dt} = Hw^n - kw^m$$

where H and k are coefficients of anabolism and catabolism respectively. To make use of this equation, which is itself a theoretical model of an open system, it is necessary to define the powers n and m. Following general physiological concepts von Bertalanffy suggests that the rate of anabolism could be assumed proportional to the resorption rate of nutritive material and therefore proportional to the magnitude of the resorbing surfaces, whereas the rate of catabolism could be taken as proportional to the total mass being broken down—that is, a constant percentage of body material is broken down per unit time. The above equation can now be written in the form

$$\frac{dw}{dt} = Hs - kw \qquad \text{.. .. .. ..} \qquad (3.4)$$

where s refers to the effective physiological surface of the organism, and the coefficients become

H = rate of synthesis of mass per unit 'physiological surface'

and k = rate of destruction of mass per unit mass.

Finally, it is necessary to express both s and w in terms of the linear dimension, l, of the organism. If it is assumed that the organism is growing isometrically and has a constant specific gravity (as is true to a close approximation in the majority of fish, see §16.1), then we can write

$$s = pl^2$$

$$w = ql^3$$

where p and q are constants.

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*Von Bertalanffy's theory of organic growth has been the subject of numerous papers, but those specified above contain the basic concepts. The account given here is a very abbreviated version of von Bertalanffy's treatment, based mainly on his 1938 paper. A geometrical interpretation of the pattern of growth in length similar to that given by von Bertalanffy's equation has been developed independently by Ford (1933) and Walford (1946).

Therefore

$$\frac{dw}{dt} = \frac{d(ql^3)}{dt} = 3ql^2\frac{dl}{dt}$$

and substitution in (3.4) gives

$$\frac{dl}{dt} = \frac{Hpl^2}{3ql^2} - \frac{kql^3}{3ql^2} = \frac{Hp}{3q} - \frac{kl}{3}$$

Putting

$$\frac{Hp}{3q} = E \quad \text{and} \quad \frac{k}{3} = K$$

we have the equation

$$\frac{dl}{dt} = E - Kl$$

the solution of which is

$$l_t = \frac{E}{K} - \left(\frac{E}{K} - L_0\right)e^{-Kt}$$

where L_0 is the length of the organism at zero age, and e is the base of the natural (Naperian) logarithm.* Now, as $t \to \infty$, $l_t \to E/K$; that is, as the organism increases in age its length increases to an asymptote which is the greatest possible length that the organism, under the given conditions, can attain. We shall denote this maximum length by L_∞, so that the previous equation becomes

$$l_t = L_\infty - (L_\infty - L_0)e^{-Kt} \quad .. \quad .. \quad .. \quad .. \quad (3.5)$$

The corresponding equation for growth in weight is obtained by substituting w in terms of l in the above expression, giving

$$w_t = \{W_\infty^{1/3} - (W_\infty^{1/3} - W_0^{1/3})e^{-Kt}\}^3 \quad .. \quad .. \quad (3.6)$$

where W_∞ and W_0 are the weights corresponding to lengths L_∞ and L_0.

Since the constant K in the above equation is simply one-third of the originally specified constant k, it is therefore proportional to the rate of destruction of body materials per unit weight and time. Having in mind the fact that the greater part of catabolism involves protein breakdown, von Bertalanffy (1934) took the rate of nitrogen excretion of certain starving animals (including fish) as a measure of their catabolic rate, and was able to obtain experimental estimates of the destruction coefficient K which agreed well with those obtained by fitting the growth equation to data referring to the growth of that animal. This fact, as von Bertalanffy points out, is substantial evidence that the coefficient K has physiological significance. A further discussion of the parameters K and W_∞ is given in §9.4.1 in connection with an analysis of the relationship between growth and food consumption.

The mathematical operations involved when incorporating von Bertalanffys' equation for growth in weight into population models can be simplified by making a slight modification to (3.6) above. In the form derived by von Bertalanffy the equation contains a constant, W_0, specifying the weight of the organism at zero time ($t = 0$). This constant is not determined directly from observation, but is obtained by fitting the growth equation to data of weight-at-age. However, the constants K and W_∞ can be used to specify an age t_0 at which the organism, with the same growth pattern as that observed in later life, would have been of zero weight. Thus, putting $w_t = 0$, and $t = t_0$ in (3.6) gives

$$W_0 = W_\infty(1 - e^{Kt_0})^3$$

---

*In this paper the symbol e is used exclusively *to denote the base of the natural (Naperian) logarithm.*

and substituting in (3.6) we have

$$w_t = W_\infty(1 - e^{-K(t-t_0)})^3 \quad \ldots \quad \ldots \quad \ldots \quad (3.7)$$

Similarly (3.5) becomes

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \quad \ldots \quad \ldots \quad \ldots \quad (3.8)$$

By expanding the cubic term of (3.7) the equation can be written in a form suitable for the integration necessary later, viz.:

$$w_t = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (3.9)$$

where

$$\Omega_0 = +1$$
$$\Omega_1 = -3$$
$$\Omega_2 = +3$$
$$\Omega_3 = -1$$

In practice, the constant t_0 must be regarded as quite artificial because the adult growth pattern is never found at the earliest age; thus in flat fish growth is not isometric until after metamorphosis, when the fish may be some months old. As we have stated previously however, we are not concerned with a representation of growth during the earliest phases of life, and there is no objection to the use of (3.7) and (3.8) provided the arbitrary nature of t_0 is borne in mind.

We have found that (3.7) and (3.8) give a very satisfactory fit to weight-at-age data for North Sea plaice and haddock, and evidence of their more general applicability to fish is given in §16.2.3. The general shape of the curve given by (3.7) is that of an asymmetrical sigmoid, as is required in practice, an example of which is shown in Fig. 3.1.The inflexion always occurs at a value of $w = 0.296\ W_\infty$.

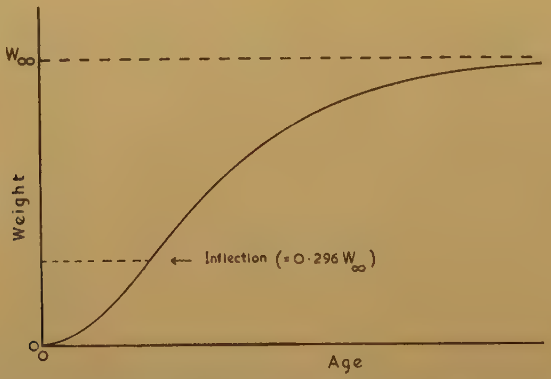

FIG. 3.1 THE VON BERTALANFFY GROWTH CURVE

[This is the general form of the curve given by the von Bertalanffy equation (3·7) for growth in weight of an organism showing the characteristic S-shape with an inflexion a little less than one-third (0·296) of the asymptotic weight.]

For the simple population models we assume that single values of the constants W_∞ and K will suffice to describe growth of the individual between ages t_ρ and t_λ, so that the growth pattern is constant in the sense defined above. Strictly speaking, this implies that all individuals of a given age are the same size, but in the simple case it will be possible to regard those values as referring to the mean weight of all individuals at each age, including both sexes. Certain cases where this is not permissible are discussed in Part II, and include the analysis of certain aspects of recruitment (§9.3), and a treatment of the case in which the two sexes having different growth rates also have differing liabilities to capture or different natural mortality rates (§11.2). In some species the onset of maturity introduces a discontinuity in the growth curve, and more than one pair of values of W_∞ and K may then be necessary to give an adequate fit to data (§9.2), although this phenomenon does not seem to be important in either plaice or haddock. Finally, for the simple treatment, we assume that the growth parameters W_∞ and K remain constant from one year to the next and, in particular, are not affected by variations in population density, so that the supply of food to any fish of the population in question can be regarded as unaffected by the abundance of the latter. The variation of growth with population density is discussed further in §9.4.

SECTION 4:

A SIMPLE MODEL GIVING THE ANNUAL YIELD IN WEIGHT FROM A FISHERY IN A STEADY STATE

Making use of the mathematical formulations given in the previous section we can now construct an analytical population model which eliminates the direct component of interdependence between the four primary factors.

4.1 THE YIELD FROM ONE YEAR-CLASS DURING ITS FISHABLE LIFE-SPAN

We consider first a single year-class reaching age t_ρ at which the fish enter the exploited area and become liable to encounters with fishing gear. For the general case we assume that the selective characteristics of the gear are such that fish become liable to capture at some higher age $t_{\rho'}$. From age t_ρ to age $t_{\rho'}$ the year-class is therefore being decreased in numbers by natural mortality only, and from (3.1) we have

$$\frac{dN}{dt} = -MN$$

Solving this equation gives the number remaining at any age t as

$$N_t = (\text{constant}) \times e^{-Mt}$$

Now, when $t = t_\rho$, $N_t = R$ by definition, so that

$$N_t = Re^{-M(t-t_\rho)} \qquad \ldots \quad \ldots \quad \ldots \qquad (4.1)$$

We wish to find the number remaining at age $t_{\rho'}$, which is obtained by substituting $t_{\rho'}$ for t in (4.1). Hence

$$N_{t_{\rho'}} = R' = Re^{-M\rho} \qquad \ldots \quad \ldots \quad \ldots \qquad (4.2)$$

where

$$\rho = t_{\rho'} - t_\rho$$

After age $t_{\rho'}$, fish will be subject to both a natural mortality and a fishing mortality, and from (3.1) and (3.2) we have

$$\frac{dN}{dt} = -\Big(F+M\Big)N$$

valid for $t_{\rho'} \leqslant t \leqslant t_\lambda$, the solution of which gives the number remaining between ages $t_{\rho'}$ and t_λ as

$$N_t = R'e^{-(F+M)(t-t_{\rho'})} \qquad \ldots \quad \ldots \quad \ldots \qquad (4.3)$$

The weight of the individual at any age t between $t_{\rho'}$ and t_λ is given, from (3.9), by

$$w_t = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)}$$

so that the total weight of the year-class at this age is

$$N_t w_t = R' W_\infty e^{-(F+M)(t-t_{\rho'})} \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)}$$

Now the rate at which fish are being caught is the same as the rate of decrease due to fishing (3.2), except that the sign is positive. Denoting the yield in weight by Y_W, the rate of yield in weight from the year class is therefore

$$\frac{dY_W}{dt} = F \, . \, N_t w_t$$

and substituting for N_t and w_t gives

$$\frac{dY_W}{dt} = FR' W_\infty e^{-(F+M)(t-t_{\rho'})} \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)}$$

Grouping terms containing t gives

$$\frac{dY_W}{dt} = FR' W_\infty e^{(F+M)t_{\rho'}} \sum_{n=0}^{3} \Omega_n e^{nKt_0-(F+M+nK)t}$$

and the yield obtained from the year-class throughout its *fishable life-span*, i.e. between ages $t_{\rho'}$ and t_λ, is obtained by integrating with respect to t between these limits, that is

$$Y_W = FR' W_\infty e^{(F+M)t_{\rho'}} \sum_{n=0}^{3} \Omega_n e^{nKt_0} \int_{t_{\rho'}}^{t_\lambda} e^{-(F+M+nK)t} \, dt$$

Finally, substituting for R' from (4.2) and integrating gives*

$$Y_W = FRW_\infty e^{-M\rho} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK} \left(1 - e^{-(F+M+nK)\lambda}\right) \quad \ldots \quad (4.4)$$

where

$$\lambda = t_\lambda - t_{\rho'} = \text{the fishable life-span}$$

Now the total annual yield from the population is the sum of the yields from each of its constituent year-classes during one year of life. Since we are supposing that the population is in a steady state (and, in particular, is receiving the same number of recruits each year), the total annual yield from it is the same as the yield throughout the fishable life-span of any one of the constituent year-classes and hence is also given by (4.4). This fact has been realised by several of the authors previously mentioned, and also by W. F. Thompson (1937), but it is convenient to give in §4.2 a proof for the particular model we are postulating, since to do so demonstrates the use of summation methods which are indispensable for the analysis of certain problems to be considered later in Part II.

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*This is the yield equation described by Graham (1952) and of which a brief derivation has been given by Beverton (1953).

Before proceeding, however, it is necessary to consider briefly our use of the expression 'steady state', since Lack (1951) has objected to Nicholson's use of the comparable term 'balance' on the grounds that it overstresses the stability of the system in question. He suggests 'restricted fluctuations' as an alternative, pointing out that " . . .compared with the increase and decrease of which they are theoretically capable, animal populations in nature show extremely small fluctuations, with a marked tendency to return to the *status quo*:"; but this invites confusion with damped oscillations, and lays stress—wrongly for the present purpose—on the aspect of change. Our use of the phrase 'steady state' is intended to convey the meaning of general stability rather than of precise constancy, even though it is the latter that is implied in most deductions from our deterministic theoretical models (except those of §6.2 where variability is considered specifically). Thus when we refer to a population or fishery as being in a steady state we mean primarily that it is not in the process of changing, either in character or size; the term allows for the existence of fluctuations with a periodicity of one year, and also for the year to year variations caused by fluctuations in factors such as the annual recruitment (which will inevitably be present), provided they are not excessive. The meaning intended will, we hope, be clear from the context and ambiguity should not arise from unqualified use of the term.

4.2 THE ANNUAL YIELD FROM THE WHOLE POPULATION

With the same simplifications as before, we now extend the above treatment to derive the annual yield from a population in a steady state in which R' fish become liable to capture on the same date each year at age $t_{p'}$.

Designating those of the first year-class to be considered by R'_0, then the number present after any time ϕ* during the first year following the date on which they become liable to capture, is

$$R_0'e^{-(F+M)\phi}.$$

At the end of this year, when $\phi = 1$, the number remaining will be

$$R_0'e^{-(F+M)}$$

and at this moment they will be joined by the second year-class R'_1. The number present after any time ϕ during the second year will therefore be

$$(R_0'e^{-(F+M)} + R_1')e^{-(F+M)\phi}$$

and at any time ϕ during the third year the number present will be

$$(R_0'e^{-2(F+M)} + R_1'e^{-(F+M)} + R_2')e^{-(F+M)\phi}$$

Since all surviving fish die after reaching age t_λ, the population will build up until, if we take λ as a whole number of years, the λth year is reached, after which it will have reached a steady state. Now the number present after time ϕ during the λth year is

$$(R_0'e^{-(F+M)(\lambda-1)} + R_1'e^{-(F+M)(\lambda-2)} + \ldots.\text{etc.}\ldots.\, R_\lambda{}'_{-2}\,e^{-(F+M)} + R_\lambda{}'_{-1})\,e^{-(F+M)\phi}$$

and since we are supposing that $R_0' = R_1', = \ldots.\text{etc.}\ldots. = R_\lambda{}'_{-2} = R_\lambda{}'_{-1}$, this expression is also true for any subsequent year and may be written in the form

$$N_\phi = R'e^{-(F+M)\phi}\sum_{q=0}^{\lambda-1} e^{-(F+M)p} \qquad \ldots \quad \ldots \quad \ldots \qquad (4.5)$$

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*The variable ϕ is used here and elsewhere as a 'dummy' time variable, and denotes a period of time of one year or less. It is measured in units of a fraction of a year, and can therefore take all positive values between zero and unity.

The weight of an individual belonging to the qth year-class of the above population at any time during the year will be

$$w_\phi = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_{\rho'} - t_0 + q + \phi)}$$

where q is an integer, ($q = 0$ for the first, or youngest, year-class). The total weight of the equilibrium population after any time ϕ of a year is therefore

$$N_\phi w_\phi = R' W_\infty \sum_{n=o}^{3} \Omega_n e^{-(F+M+nK)\phi - nK(t_{\rho'} - t_0)} \sum_{q=o}^{\lambda - 1} e^{-(F+M+nK)q}$$

The rate of yield in weight after this time is

$$\frac{dY_W}{d\phi} = FR' W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_{\rho'} - t_0)} \sum_{q=0}^{\lambda - 1} e^{-(F+M+nK)q - (F+M+nK)\phi}$$

Integrating with respect to ϕ from $\phi = 0$ to $\phi = 1$ and making the second summation, gives

$$Y_W = FR' W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK} \left(1 - e^{-(F+M+nK)\lambda}\right)$$

This equation is identical to (4.4).

The annual yield in number, Y_N, can be derived in a similar way, but with all reference to growth omitted. Thus from (4.5) the rate of yield in number is

$$\frac{dY_N}{d\phi} = FR' \sum_{q=0}^{\lambda - 1} e^{-(F+M)q - (F+M)\phi}$$

from which

$$Y_N = \frac{FR'}{F + M} \left(1 - e^{-(F+M)\lambda}\right) \quad .. \quad .. \quad .. \quad (4.6)$$

It should be remembered that the annual yield from a population is, strictly, only the same as the yield from any one of the year classes of which that population is composed, fished throughout its fishable life-span, under truly constant conditions, and it will not be exactly true if any of the coefficients vary in magnitude from one year to the next. An important case of this type concerns the analysis of the transitional phase following a sudden change in fishing intensity or gear selectivity (see 8.2) by summation methods similar to the above. The method of §4.1 can, however, be used to analyse cases in which the population parameters vary with density or with age, provided steady states are considered. It may be noted that (4.4) gives the yield over any period of a year's duration, that is, commencing on any date, even though fish may not reach either age $t_{\rho'}$ or t_λ on this date, and λ may not be a whole number of years. Finally, although it has been assumed that the recruitment of a year-class to the exploited area and its entry to the exploited phase takes place instantaneously at ages t_ρ and $t_{\rho'}$ respectively, it can be shown that the same equations are obtained if these events are spread over a period of time, provided the time-function remains the same each year (see also §8.3.1).

SECTION 5: ADAPTATION OF THE SIMPLE MODEL TO GIVE OTHER CHARACTERISTICS OF THE CATCH AND POPULATION

In a study of an exploited fish population there are several quantities, besides the annual yield in weight, that will require assessment. From the economic aspect it is necessary to know the catch per unit effort, and, probably, the mean weight of fish in the catch, while the analysis of situations in which factors such as natural mortality and growth vary with the population density (discussed in Part II of this paper) requires expressions giving the numbers and biomass of the population. Finally, when the behaviour of population models comes to be tested by observation or experiment, or they are used as an adjunct to fishery management, it is of help to obtain from the models predicted values of certain quantities such as the mean length and mean age of fish in the catch, which are directly estimated from samples. To establish the equations giving the above characteristics we use the same definitions and assumptions as in the previous section, and it will be seen that the same general methods are applicable.

5.1 Annual Catch per Unit Effort

It was mentioned in §3.3 that in many circumstances the fishing mortality coefficient F can be taken, to a first approximation, as proportional to the total fishing effort, g, expended per year. If the size of the exploited area over which that effort is distributed is A, then we have from (3.3)

$$F = \frac{cg}{A}$$

Consequently, the annual catch per unit fishing effort is, in these circumstances, proportional to the annual catch per unit fishing mortality coefficient, since we can write

$$Y_W \frac{A}{cg} = \frac{Y_w}{F} \quad \text{.. .. .. ..} \quad (5.1)$$

Hence dividing (4.4) by F and substituting in (5.1) gives the catch per unit effort as

$$\frac{Y_W}{g} = \frac{C}{A} R' W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{p'} - t_0)}}{F + M + nK} \left(1 - e^{-(F+M+nK)\lambda}\right) \quad \text{.. ..} \quad (5.2)$$

5.2 Population Number

If we denote by N_ϕ the number of fish present after time ϕ has elapsed following the commencement of the year,* then the *annual mean number*, $\bar{P}_N$, present during that year is given by the expression

$$\bar{P}_N = \frac{\int_0^1 N_\phi \, d\phi}{\int_0^1 d\phi}$$

However, the quantity $\int_0^1 d\phi = 1$, so that we may omit the denominator from this and other expressions giving the annual mean value of characteristics. For the section of the population liable to capture, i.e. that between ages $t_{\rho'}$ and t_λ, the function N_ϕ is given by (4.5), so that we have the annual mean number in this section of the population given by

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*In what follows we may, without loss of generality assume that we are dealing with the case in which ages t_p, $t_{p'}$ and t_λ are integral numbers of years apart, and that the year commences on the date on which all these ages are reached, thereby enabling the equations to be developed in the simplest possible way.

$$\begin{aligned}\bar{P}_N' &= R'\sum_{q=0}^{\lambda-1} e^{-(F+M)q}\int_0^1 e^{-(F+M)\phi}d\phi \\ &= \frac{R'}{F+M}\left(1-e^{-(F+M)\lambda}\right) \quad .. \quad .. \quad .. \qquad (5.3)\end{aligned}$$

Similarly, the annual mean number between ages t_ρ and $t_{\rho'}$ is given by the expression

$$R\sum_{q=0}^{\rho-1} e^{-Mq}\int_0^1 e^{-M\phi}d\phi = \frac{R}{M}\left(1-e^{-M\rho}\right) \quad .. \quad .. \qquad (5.4)$$

The annual mean number of the whole population present in the exploited area is therefore given by the sum of (5.3) and (5.4), as

$$\bar{P}_N = R\left\{\frac{1-e^{M\rho}}{M} + \frac{e^{M\rho}\left(1-e^{-(F+M)\lambda}\right)}{F+M}\right\} \quad .. \quad .. \qquad (5.5)$$

5.3 Population Biomass

With the same simplifications as in §5.2, the annual mean biomass, $\bar{P}_W$, is given by

$$\bar{P}_W = \int_0^1 N_\phi w_\phi \, d\phi$$

Substituting for $N_\phi w_\phi$ from (4.6) we have, for the section of the population liable to capture (i.e. the exploited phase),

$$\begin{aligned}\bar{P}_W' &= R'W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_{\rho'}-t_0)} \sum_{q=0}^{\lambda-1} e^{-(F+M+nK)q}\int_0^1 e^{-(F+M+nK)\phi}d\phi \\ &= R'W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\left(1-e^{-(F+M+nK)\lambda}\right) \quad .. \qquad (5.6)\end{aligned}$$

and, similarly, for that section of the population between ages t_ρ and $t_{\rho'}$, the annual mean biomass is

$$RW_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_\rho-t_0)}}{M+nK}\left(1-e^{-(M+nK)\rho}\right) \quad .. \quad .. \qquad (5.7)$$

The annual mean biomass of the whole population in the exploited area is therefore the sum of (5.6) and (5.7), i.e.,

$$\begin{aligned}\bar{P}_W = RW_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_\rho-t_0)}\bigg\{&\frac{1-e^{-(M+nK)\rho}}{M+nK} + \\ &+ \frac{e^{-(M+nK)\rho}\left(1-e^{-(F+M+nK)\lambda}\right)}{F+M+nK}\bigg\} \quad .. \quad .. \qquad (5.8)\end{aligned}$$

It will be noticed that (5.6) is identical to (5.1) so that for a given exploited area, the catch per unit effort is proportional to the annual mean biomass of the exploited phase. This relationship in fact follows from the assumptions which have been made concerning the form of the fishing mortality, and is in wide use in fishery research, though the extent to which catch per unit effort can be used as an index of the abundance of the whole population in the exploited area depends upon the magnitude of ρ in (5.8). A discussion of the conditions under which this relationship does *not* hold will be found in §§8.3.2 and 10.2.3.2.

5.4 MEAN LENGTH AND WEIGHT OF FISH IN THE CATCH

By the methods of §4.1, we have that the total length of all fish caught per year is given by the expression

$$F\int_{t_{\rho'}}^{t_\lambda} N_t l_t \, dt$$

and that the *total number* of fish caught per year is given by

$$Y_N = F\int_{t_{\rho'}}^{t_\lambda} N_t \, dt \qquad \ldots \quad \ldots \quad \ldots \qquad (5.9)$$

so that the *mean length of fish in the annual catch* is

$$\bar{L}_y = \frac{\int_{t_{\rho'}}^{t_\lambda} N_t l_t \, dt}{\int_{t_{\rho'}}^{t_\lambda} N_t \, dt} \qquad \ldots \quad \ldots \quad \ldots \qquad (5.10)$$

Substituting for l_t and N_t from (3.8) and (4.3) respectively, gives

$$\bar{L}_y = L_\infty \left\{1 - \frac{(F + M)(1 - e^{-(F+M+K)\lambda})}{(F + M + K)(1 - e^{-(F+M)\lambda})} e^{-K(t_{\rho'} - t_0)}\right\} \qquad \ldots \qquad (5.11)$$

Similarly, the *mean weight* of fish in the annual catch is

$$\bar{W}_y = \frac{Y_W}{Y_N}$$

and substituting from (4.4) and (5.9) gives

$$\bar{W}_y = \frac{(F + M)W_\infty}{1 - e^{-(F+M)\lambda}} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F+M+nK)\lambda}\right) \qquad (5.12)$$

5.5 MEAN AGE OF FISH IN THE POPULATION AND CATCH

Following the same method as in §5.4 the mean age of fish in the population is

$$\bar{T} = \frac{\int_{t_\rho}^{t_\lambda} t N_t \, dt}{\int_{t_\rho}^{t_\lambda} N_t \, dt}$$

$$= \frac{\dfrac{1}{M}\left\{t_\rho - t_{\rho'}e^{-M\rho} + \dfrac{1}{M}\left(1 - e^{-M\rho}\right)\right\} + \dfrac{e^{-M\rho}}{F+M}\left\{t_{\rho'} - t_\lambda e^{-(F+M)\lambda} + \dfrac{1}{F+M}\left(1 - e^{-(F+M)\lambda}\right)\right\}}{\dfrac{1}{M}\left(1 - e^{-M\rho}\right) + \dfrac{e^{-M\rho}}{F+M}\left(1 - e^{-(F+M)\lambda}\right)} \tag{5.13}$$

Similarly, the mean age of the fish in the annual catch is

$$T_y = \frac{1}{F+M} + \frac{t_{\rho'} - t_\lambda e^{-(F+M)\lambda}}{1 - e^{-(F+M)\lambda}} \quad \ldots \quad \ldots \tag{5.14}$$

It will be seen that these two equations become identical when $\rho = 0$, and that the mean age of fish in the annual catch is always the same as that in the exploited phase of the population. By the methods of §6.2 it can be shown that this latter statement remains true irrespective of the occurrence of fluctuations in the annual number of recruits. Similarly, the representation of the fishing mortality adopted in §3.3 results in the catch having the same age-composition as the population—again irrespective of fluctuations in recruitment.

PART II

Some Extensions of the Simple Theory of Fishing

> "*At length everything is brought to its utmost limit of growth by nature, the creatress and perfectress. This is reached when what is poured into its vital veins is no more than what drains away. Here the growing-time of everything must halt. Here nature checks the increase of her own strength*".
>
> LUCRETIUS, *The Nature of the Universe* (Trans. R. E. Latham)

In Part I were developed theoretical models giving the annual yield and other characteristics of the catch and population under steady conditions in terms of the four primary factors of recruitment, natural and fishing mortalities, and growth. We refer to these as simple population models because the mathematical form in which the primary factors have been represented is the simplest that would seem to be in reasonable accordance with the general characteristics of North Sea demersal fish populations. When discussing in §2 the simplifying assumptions on which these models were based, some indications were given of the more complex situations that are likely to be found when a detailed study is made of a particular population and its associated fishery to enable, for example, assessment of the probable value of a specific proposal for regulation. The main purpose of Part II is therefore to re-examine those assumptions with a view to elaborating and extending the population models to take into account some of those phenomena that data have shown to exist, or which, by analogy with the behaviour of other natural populations, are likely to exist.

For the most part we shall be concerned, as in Part I, with the analysis of a single homogeneous population, and usually it will be sufficient to derive population models in a form giving the annual yield in weight, since the modifications required to obtain other characteristics of the catch and population can readily be seen by reference to the methods of §5. There are three main phenomena found in connection with all four primary factors, which can cause the actual behaviour of a fishery to depart from that predicted from the simple model. They are, firstly, variation in magnitude of parameters with age of fish; secondly, variation with time, of which year-to-year variation, as opposed to cyclic seasonal change, is the more important; and thirdly, variation with population density, including both intra- and inter-specific interaction of various kinds. This last is perhaps the most important of the three, since it is responsible for the indirect component of interdependence of the primary factors which, as was mentioned in §2, is not taken into account in the simple models. We have found it convenient to discuss these with reference to each factor separately in the order presented in Part I; thus §§6, 7, 8 and 9 correspond to §§3.1, 3.2, 3.3 and 3.4 respectively. The only important exception to this arrangement concerns the variation of recruitment with age; because this is primarily the result of growth differences between individuals of the same age it is most conveniently included in §9 on growth. There is, in addition, a fourth phenomenon which may, in some circumstances, be of great importance, namely spatial variation in magnitude of parameters. This involves another factor that is not incorporated in the simple models—the movement of fish within the exploited area. For this reason, and also because it is usually only spatial variation in the fishing mortality that is of practical importance, we consider this problem separately in §10. Finally, in §11, we discuss briefly some problems arising in fisheries based on mixed populations. As typical examples we consider the case of a fishery based on two interacting populations, both of which are caught simultaneously by the same fishing gear, and of heterogeneity within a single species caused by phenomena such as the differential behaviour of the two sexes.

The advantage of discussing the variation of parameters with age, time and population density with respect to each factor in turn, is that the simple representations of Part I can be retained for the remaining three factors, thus enabling the complexity of the resulting population models to be kept to the minimum. In practice, it is true, we should expect to find these phenomena present in two or more factors simultaneously, but there are no particular theoretical difficulties in combining the separate treatments to represent situations of this kind, and we do not discuss the subject under a separate heading. Certain problems arise, however, in the determination of parameters from data and in computational work based on models containing factors varying simultaneously, and these are each discussed in the appropriate section later in the paper (see e.g. §§14.3.1, 16.4.1.3 and 18.5).

SECTION 6: RECRUITMENT AND EGG-PRODUCTION

Hitherto, the method of representing the life-cycle has been to take the entry of fish into the exploited area as the arbitrary starting point, and to make the simplification that a constant number of recruits enter the exploited area each year. In this section we complete the life-cycle by tracing survival from the egg to the recruit stage (§6.1.1), and then express the total number of eggs spawned in a given year in terms of the adult population that produced them (§6.1.2). This leads to the development of 'self-regenerating' population models in which the life-cycle has no arbitrary starting point (§6.1.3), and raises important problems concerning the stability of fish populations.

It will be noted that the analysis of pre-recruit mortality is carried through without reference to the recent paper by Ricker (1954) on "Stock and Recruitment". This important contribution appeared after the final draft of this section had been prepared. However, as Ricker's studies, whilst conducted on lines closely parallel with our own, led him to conclusions differing from ours in some respects, it seemed desirable to outline for the reader's guidance the areas of agreement and disagreement between our results. Accordingly, an explanatory paragraph has been added at the end of §6.1.1.

The other aspect of recruitment we consider is the fluctuation in annual recruit numbers resulting from factors other than variation in the size of the adult population (§6.2). The case of recruits entering into several age-groups raises problems most conveniently discussed in detail in connection with growth (§9.3), and only a brief reference to this is made here (§6.1.4).

6.1 The Dependence of Recruit Numbers on the Size of the Adult Population

6.1.1 *A theoretical analysis of larval and pre-recruit mortality*

Little is known about the population dynamics of many marine fish during very early life, but there are nevertheless certain general facts concerning North Sea demersal fish which are of some help in theoretical analysis of larval mortality.

(i) The general indications from the behaviour of many species are that there is no marked relationship between the abundance of spawners and the number of subsequent recruits, within the range of population size for which data are available. It has to be remembered, however, that the presence of extremely large fluctuations in recruit numbers from other causes would tend to obscure anything but a fairly pronounced relationship, unless data from a very long series of years were available.

(ii) The populations in question seem to be inherently stable under the intensities of fishing which have so far been exerted; that is, they do not seem to be proceeding either to extinction or to an infinitely great size. We can take it that these populations are also stable in the virgin state. In the absence of detailed information to the contrary, we would suggest that general evidence of population stability forms a valuable guide to an adequate formulation of theoretical population models.

(iii) It is known that larval mortality is extremely high, and possibly occurs mainly at certain critical stages in early life. One such may coincide with the exhaustion of the yolk-sac when the larva, for the first time, becomes dependent on its own ability to obtain particular kinds of food and on the abundance of the latter in the immediate environment. Another critical phase may be at metamorphosis, especially in flatfish (Pleuronectidae), where there is very considerable anatomical reorganisation. The only definite measurements of larval mortality rates that are known to us are those of Sette (1943a) on the Atlantic mackerel (*Scomber scombrus*), which suggest that in this species there is an increase in the mortality rate when the yolk-sac is exhausted. There is also some evidence that larvae are sensitive to the physical characteristics of the environment; Carruthers *et al.* (1951), for example, have stated that the direction of the prevailing winds may influence the survival of larval haddock and herring, and Walford (1946a) has demonstrated the existence of a correlation between brood strength and salinity in the California sardine (*Sardinops caerulea*) though in this case salinity is not the direct cause of mortality but is a phenomenon associated with the real cause—upwelling and plankton production. Walford (1938) has also shown that certain currents can result in the eggs of the Georges Bank haddock being carried into an environment unfavourable for the survival of the fry, and that this factor may have been the cause of the small size of the 1932 year-class in this species.

Taking these facts as a starting point we shall attempt a theoretical analysis of larval mortality which is conveniently presented in two stages. In §6.1.1.1 is given in some detail a treatment of what would seem to be the simplest and most generally applicable relationship between egg-production and subsequent recruit numbers that leads to a population behaviour in agreement with the above statements; while in §6.1.1.2 we indicate briefly how certain other phenomena, which might be of importance in special cases, may be taken into account and the kind of effects they would produce.

6.1.1.1 *Direct density dependence*

What might appear to be the simplest reasonable assumption concerning larval mortality is that it could be described by the same equation that we have previously used for the natural mortality of the post-recruit phase of the population, viz.

$$ {}_{M}\left(\frac{dN}{dt}\right) = -MN $$

If we define by E the total number of eggs laid during a given spawning season, then the subsequent number of recruits according to the above equation is

$$ R = Ee^{-Mt_p} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.1) $$

which gives a proportional relationship between E and R. But it can readily be shown that this conclusion is untenable if we are to have a population which would remain stable if a permanent change in the magnitude of any factor influencing egg production or pre-recruit mortality took place.

Suppose we have, initially, an equilibrium population with only one age-group in the exploited phase. If E_0 eggs are being laid each year, and a constant number of recruits, R_0, are surviving from them, then from (6.1) we can put

$$ R_0 = aE_0 \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.2) $$

where a is a constant. Further, for the population to remain in equilibrium, each group R_0 of recruits must lay a total of E_0 eggs during the course of their life, and we can write

$$ E_0 = \gamma R_0 \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.3) $$

where γ is the number of eggs laid per recruit. The value of γ depends, *inter alia*, on the magnitude of the fishing mortality, but under equilibrium conditions is of course equal to $1/a$. Suppose now that immediately after a given group, R_0, of recruits enters the population, a sustained *decrease* occurs in the production of eggs per recruit, to a lower value γ' (such as would result, for example, from a sudden change in fishing mortality to a higher level with consequent reduced survival of fish in the adult population). The resulting total number of eggs, E_1 (where $E_1 < E_0$), is therefore given by

$$E_1 = \gamma' R_0 \qquad \text{(6.4)}$$

These give rise to R_1 recruits such that, from (6.2)

$$R_1 = aE_1 \qquad \text{(6.5)}$$

and these recruits to E_2 eggs, where

$$E_2 = \gamma' R_1 \qquad \text{(6.6)}$$

and the E_2 eggs, in turn to R_2 recruits, where

$$R_2 = aE_2 \qquad \text{(6.7)}$$

Now, from (6.4) and (6.5) we have

$$\frac{R_1}{R_0} = a\gamma' = \text{constant}$$

and from (6.6) and (6.7)

$$\frac{R_2}{R_1} = a\gamma' = \frac{R_1}{R_0}$$

so that, in general,

$$\frac{R_n}{R_0} = (a\gamma')^n$$

The numbers in successive annual groups of recruits therefore form a geometric series with constant ratio $a\gamma'$. This ratio is less than unity, since $a = 1/\gamma$ and $\gamma' < \gamma$, so that the series is decreasing. Successive recruit groups therefore contain continually decreasing numbers of fish, and eventually the annual number of recruits becomes zero, and the population extinct. In exactly the same way it can be shown that an *increase* in the number of eggs laid per recruit (e.g. caused by a decrease in fishing mortality) would result in the population becoming infinitely great, since in this case $a\gamma' > 1$. Furthermore, a similar behaviour is shown by a population having more than one exploited age-group, except that the population trend, in either direction, is slower.

This behaviour is illustrated in Figs. 6.1 and serves to introduce a diagrammatic method which we shall use when discussing more complex situations later in this section. We need to distinguish two relationships in these diagrams, that giving the number of recruits surviving from a given number of eggs and that giving the number of eggs produced by those recruits. With the above hypothesis both relationships are taken as proportional, with coefficients a and γ respectively, so that if we have initially a steady state in which R_0 recruits survive from E_0 eggs and then, in turn, produce E_0 eggs, the two lines (which we call the recruitment curve and the egg-production curve) will be coincident. This is shown in Fig. 6.1.1. In Fig. 6.1.2 we suppose that a sustained decrease in egg-production per recruit takes place, so that this line is no longer coincident with the recruitment curve (slope a) and has a slope γ' (broken line). The subsequent trends in egg-production and recruitment are shown on the $R - E$ diagram and plotted against time in its lower part. Fig. 6.1.3 shows in a similar way the events following an increase in egg-production per recruit. From the above discussion it will be appreciated that these trends are exponential in form. In practice, large fluctuations in pre-recruit mortality, i.e. in the magnitude of the coefficients M and a of (6.1) and (6.2) respectively, might check these trends temporarily but could not arrest them permanently, and we must therefore reject (3.1) as not giving a suitable representation of mortality during early life.

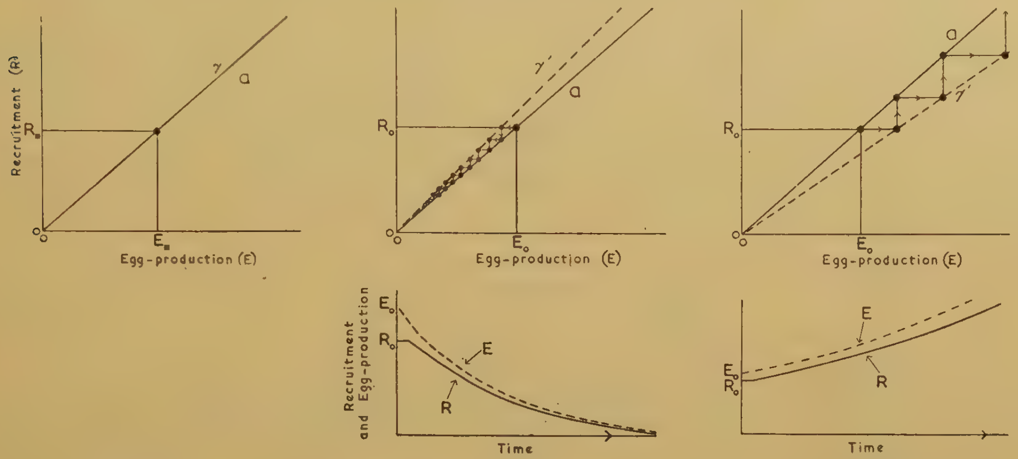

Fig. 6.1.1 Fig. 6.1.2 Fig. 6.1.3

FIGS. 6.1 THE DYNAMICS OF A SELF-REGENERATING MODEL WITH A DENSITY INDEPENDENT LARVAL MORTALITY RATE

[The upper part of each diagram shows successive values of recruitment and egg-production following a sustained change in egg-production per recruit of the adult population; in the lower part these are plotted as a time series. With this form of larval mortality a population cannot regain a steady state if a sustained change in egg-production per recruit occurs.]

Fig. 6.1.1 Egg-production and recruitment in the steady state.
Fig. 6.1.2 Trends following a sustained decrease in egg-production per recruit.
Fig. 6.1.3 Trends following a sustained increase in egg-production per recruit.

These objections can be overcome if we regard the mortality coefficient during one or more stages of early life as being influenced by the density of the larval fish themselves. We do not know of any data which can demonstrate this directly in the case of marine fish, but evidence from other population studies suggests that it probably occurs. The density of larvae could affect their mortality rate in many ways, but competition for a limited food supply at critical stages such as that when the yolk-sac is exhausted might be expected to be one of the most direct and important, and there is considerable evidence to show that shortage of the correct type of food at this time is probably a major cause of death (Tåning, 1951). We have previously mentioned the results obtained by Sette (1943a) for the Atlantic mackerel in this connection, and it is interesting to note that he found (p. 205) an indication of a correlation between pre-recruit mortality and abundance of zooplankton on which the young of this species feed. Ricker and Foerster (1948, p. 199) mention the work of Einsele (1941) on the fry of *Coregonus* in southern German lakes; this latter author found that a heavy mortality occurred soon after hatching, but that this could be reduced to negligible proportions by feeding the fry with plankton in excess of the supply available in the normal environment. A series of investigations by Soleim (1942) on the causes of mortality in the young of the Norwegian herring have shown that a very heavy mortality occurs when the yolk-sac is consumed, and the author concludes that this is due to a shortage of suitable food. He based this conclusion on tank experiments and on surveys of the distribution of fry in relation to that of their food; he found, for example, that large numbers of dead fry were associated with areas of low food abundance. Svärdson (1949), from a survey of work by authors other than those mentioned above, also concludes that food supply is an important factor influencing larval mortality. He cites, in particular, evidence from transplantations of pike-perch (*Lucioperca sandra*) and *Coregonus sp.* in Swedish lakes which shows that there is a definite inverse relationship between larval mortality rate and larval density, and concludes that intra-specific competition for food must be the major factor concerned.

Thus it seems clear that there may often be critical stages in the early development of fish when an adequate supply of the correct kind of food is essential to survival, and further, that in normal circumstances the supply may be far less than that necessary to prevent a heavy mortality from this cause. Owing to the tendency for young larvae to be concentrated in a relatively small area as the result of aggregation of the spawning adults, it is highly probable that the food supply to each is influenced by the number of other larvae in the immediate vicinity, thus producing a mechanism whereby the density of larvae can affect their mortality rate.* The simplest assumption we can make, and that which is in best agreement with data from many population studies (see Kostitzin, 1939), is that the mortality coefficient is itself linearly related to the population density, so that we can write, in general terms,

$${}_M\!\left(\frac{dN}{dt}\right) = -\left\{\mu_1(t) + \mu_2(t)N\right\}N \quad .. \quad .. \quad .. \quad (6.8)$$

It will be seen that the term $\mu_1(t)$ has the same significance as the coefficient M of (3.1), that is, it refers to the 'density-independent' component of mortality, whereas the term $\mu_2(t)$ can be regarded as referring to the 'interaction' between individuals of the population.

We have previously mentioned that one of the characteristics of mortality during the early life of fish is that it varies enormously with age, so that we could not expect the coefficients μ_1 and μ_2 to remain even approximately constant during the pre-recruit phase. For example, it may well be that μ_2 is virtually negligible except at certain critical stages. This variation must be taken into account when arriving at a solution for (6.8) that is of practical value. Let us suppose that the pre-recruit phase be divided into periods during each of which the coefficients μ_1 and μ_2 of (6.8) are effectively constant. There can be as many such periods as are necessary to achieve this and they need not be of equal duration. For the rth of these periods we can therefore write

$$\frac{dN}{dt} = -\left({}_r\mu_1 + {}_r\mu_2 N\right)N \quad \dagger$$

and if we suppose that the fish are of age t_r at the beginning of the rth period, then the number present at any time during the period becomes

$$N_t = \frac{1}{\dfrac{{}_r\mu_2}{{}_r\mu_1}\left(e^{{}_r\mu_1(t - t_r)} - 1\right) + \dfrac{e^{{}_r\mu_1(t - t_r)}}{N_{t_r}}}$$

where N_{t_r} is the number present at the beginning of the rth period. If we put $t = t_{r+1}$ and make the substitutions

$$\frac{{}_r\mu_2}{{}_r\mu_1}\left(e^{{}_r\mu_1(t_{r+1} - t_r)} - 1\right) = \alpha_r'$$

$$e^{{}_r\mu_1(t_{r+1} - t_r)} = \beta_r'$$

---

*A similar effect has been observed in exploited mammalian populations. Thus in some deer populations the mortality rate of fawns decreases with hunting activity owing to the reduced competition for food in a depleted stock. Again, starvation is certainly an important cause of mortality among nestling birds of some species, and depends directly on clutch size, so there is a tendency towards constancy of family size (Lack, 1948a, 1949; Lack and Silva, 1949).

†The coefficients ${}_1\mu_1$ and ${}_1\mu_2$ for the first period may be taken to define the success of fertilisation, and either may have a value of zero, according to the circumstances (see §6.1.2).

then the number surviving to the beginning of the $(r + 1)$th period is

$$N_{t_r+1} = \cfrac{1}{\alpha'_r + \cfrac{\beta'_r}{N_{tr}}} \quad \cdots \quad \cdots \quad \cdots \quad \cdots \quad \cdots \quad (6.9)$$

By the same methods we may express N_{t_r} in terms of the number present at the beginning of the $(r - 1)$th period, viz.:

$$N_{t_r} = \cfrac{1}{\alpha'_{r-1} + \cfrac{\beta'_{r-1}}{N_{t_r-1}}}$$

and substituting in (6.9) gives

$$N_{t_r+1} = \cfrac{1}{\alpha'_r + \beta'_r\left(\alpha'_{r-1} + \cfrac{\beta'_{r-1}}{N_{t_r-1}}\right)} = \cfrac{1}{\alpha'_r + \alpha'_{r-1}\beta'_r + \cfrac{\beta'_r\beta'_{r-1}}{N_{t_r-1}}}$$

By repeating this procedure we obtain

$$N_{t_r+1} = 1\Big/\Big\{\alpha'_r + \alpha'_{r-1}\beta'_r + \alpha'_{r-2}\beta'_r\beta'_{r-1} + \ldots\text{etc.}\ldots + \\ + \alpha'_0\left(\beta'_r\beta'_{r-1}\ldots\text{etc.}\ldots\beta'_1\right) + \frac{\beta'_r\beta'_{r-1}\ldots\beta'_0}{N_{t_0}}\Big\}$$

where N_{t_0} is the number present at time zero, i.e. is the total number of eggs, E. But for any given value of r we can put

$$\alpha'_r + \alpha'_{r-1}\beta'_r + \alpha'_{r-2}\beta'_r\beta'_{r-1} + \ldots\text{etc.}\ldots + \alpha'_0(\beta'_r\beta'_{r-1}\ldots\text{etc.}\ldots\beta'_1) = \alpha_r$$

and

$$\beta'_r\beta'_{r-1}\ldots\text{etc.}\ldots\beta'_0 = \beta_r$$

so that

$$N_{t_r-1} = \cfrac{1}{\alpha_r + \cfrac{\beta_r}{E}} \quad \cdots \quad \cdots \quad \text{(cf. equation (6.9))}$$

where α_r and β_r are constants. Since this argument is true for any value of r, the latter can be put equal to the total number of periods into which we have divided the pre-recruit phase. Then N_{t_r+1} is the number of fish surviving to the beginning of the post-recruit phase, i.e. the number of recruits, and we have

$$R = \cfrac{1}{\alpha + \cfrac{\beta}{E}} \quad \cdots \quad \cdots \quad \cdots \quad \cdots \quad (6.10)$$

where α and β are constants for any given value of t_ρ and given sets of values of μ_1 and μ_2.

This is the basic relationship between egg-production and recruitment which we investigate in detail below. At this stage it is of interest to note the way in which α and β are related to the two types of mortality designated by the coefficients μ_1 and μ_2; thus β contains only the μ_1's, whereas α contains both the μ_1's and the μ_2's. Now the μ_1's will be determined mainly by 'external' factors, the effects of which on the individual larvae are not dependent on their total numbers and which cause a given percentage mortality irrespective of the number of larvae present. To a first approximation factors such as temperature, wind and currents, and the abundance of predators can therefore be interpreted by changes in β only. For example, if a value β_1 is associated with a certain abundance of predators, P_1, then a change in the number of predators to P_2 where

$$P_2 = xP_1$$

will produce a value β_2 such that

$$\beta_2 \simeq \beta_1{}^x$$

provided that the increase in predatory activity affects equally all stages of the pre-recruit phase. Now from the definition of α it will be seen that the associated change in the value of this coefficient will be in the same direction as that in β, and will add to the effect on the number of recruits; a minimum estimate of the resultant effect on recruitment is therefore obtained by neglecting the change in α and computing

$$R_2 = \frac{1}{\alpha_1 + \dfrac{\beta_2}{E}}$$

Other factors, particularly the amount of food available to the larvae, will affect mainly the μ_2's, and if the latter are all affected equally the value of α will change proportionally. The theoretical analysis of the effect of fluctuating environmental conditions on the survival of young fish receives further mention in §15.2.3.2.

This representation of pre-recruit mortality as a density dependent process may best be illustrated by a numerical example. In Fig. 6.2 we have imagined a pre-recruit phase of $t_\rho = 1.2$ years split into three unequal stages during each of which the mortality coefficients are constant, though they take very different values in each, as follows:[*]

Stage	*Duration (yrs.)*	*Mortality coefficients*
1	0.3	$_1\mu_1 = 0.827$ $_1\mu_2 = 9.113 \times 10^{-10}$
2	0.025	$_2\mu_1 = 19.5$ $_2\mu_2 = 0$
3	0.875	$_3\mu_1 = 1.0$ $_3\mu_2 = 5.556 \times 10^{-10}$

The short second phase, during which there is a high 'intrinsic' mortality only (i.e. $_2\mu_2 = 0$), might be taken as corresponding to a metamorphosis in flatfish, or to the young fish reaching a stage at which they become susceptible to an unfavourable physical environment, perhaps as a result of a change in habitat. We have taken two values of E, viz.: 2×10^9 and 5×10^9, from which the survival curves, using these changing coefficients, are shown by (a) and (b) respectively. After age t_ρ it is assumed that the natural mortality can be described by (3.1), with $M = 0.1$. The important feature of Fig. 6.2 is that the two values of R, i.e. the recruits to the exploited phase, are relatively closer than the numbers of eggs of which they are the progeny and, in fact, as $E \rightarrow \infty$, R approaches a finite limit. Putting $E = \infty$ in (6.10) gives this limit as

$$R = \frac{1}{\alpha}$$

and in the example of Fig. 6.2 this value is 5.02×10^8.

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[*] It is of interest to find that the trends in the larval mortality rate postulated in Fig. 6.2 are similar to those observed by Allen (1951, Fig. 5) during the early life of trout of the Horokiwi stream.

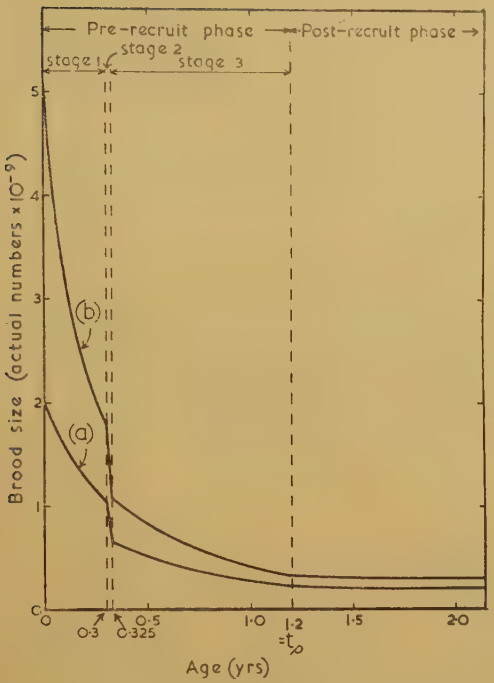

FIG. 6.2 PRE-RECRUIT SURVIVAL CURVES WITH THE LARVAL MORTALITY RATE VARYING LINEARLY WITH DENSITY (6.8)

[These are hypothetical examples in which the mortality rate is taken as changing abruptly at certain stages during the pre-recruit phase, as explained in the text. Note that the number of recruits (at age t_ρ) are more similar in the two cases than are the number of eggs from which they survive; this is the result of making the larval mortality rate density dependent (see also Fig. 6.3).]

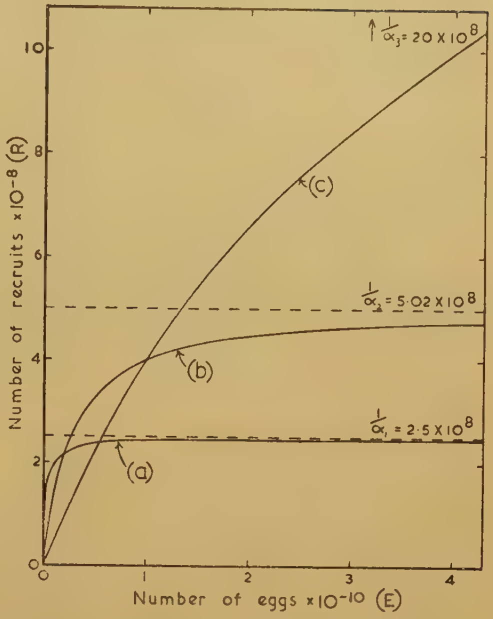

FIG. 6.3 THE RELATIONSHIP BETWEEN EGG-PRODUCTION AND RECRUITMENT WITH A LARVAL MORTALITY RATE VARYING LINEARLY WITH DENSITY (6.10)

[The differences between the three curves are the result of varying the magnitudes of the parameters α and β of (6.10), thus altering the relative importance of the density independent and density dependent components of larval mortality. Curve (a) shows how this representation of larval mortality can result in recruitment being virtually independent of egg-production over a wide range—a feature which appears to be characteristic of many fish populations.]

The general form of the relationship between R and E defined by (6.10) is shown in Fig. 6.3, using three selected pairs of values of α and β, one of which (curve (b)), is that relating R to E in Fig. 6.2. The values used are as follows:—

$$\text{curve (a)} \quad \begin{aligned} \alpha_1 &= 4 \times 10^{-9} \\ \beta_1 &= 1 \end{aligned}$$

$$\text{curve (b)} \quad \begin{aligned} \alpha_2 &= 1.99 \times 10^{-9} \\ \beta_2 &= 5.005 \end{aligned}$$

$$\text{curve (c)} \quad \begin{aligned} \alpha_3 &= 0.5 \times 10^{-9} \\ \beta_3 &= 20 \end{aligned}$$

It will be seen that the shape of the part of the $E - R$ curve illustrated is greatly changed by altering the relative magnitudes of the two coefficients. Thus if it is supposed,for purposes of illustration, that the mean egg-production of a population during an observed steady state lies somewhere near the middle of the scale of E shown in Fig. 6.3—say at about 2×10^{10}—then curve (a) gives a virtually constant recruitment over a wide range of change of egg-production relative to this mean, and yet results in a value of $R = 0$ when $E =$ zero. At the other extreme, curve (c) results in a nearly proportional change of R with

E in the region of the mean egg-production, but avoids the logical difficulties encountered if an exactly proportional relationship is postulated. It is important to note that these curves have the same general shape as those postulated by Kesteven (1947a) and Tester (1948) for the relationship between recruitment and reproductive potential.

Values of the coefficients α and β of (6.10) could be determined by fitting this equation to data of the total eggs laid annually and the number of subsequent recruits. The presence of large variations in R caused by variations in the μ's and not in E would result in average estimates of α and β being obtained and may require a long series of data in order to obtain adequate values, especially if the values of E are near the asymptote of the curve relating E and R (see Fig. 6.3). This matter is discussed further in §15.2.3.2.

It remains to show that (6.10) satisfies the requirements for population stability, and we may use the same methods as those used above to show that (6.1) was lacking in this respect, namely to analyse the changes in a population consisting of one exploited age-group only. Let us suppose that we have an initial steady state in which E_0 eggs give rise to R_0 recruits each year according to (6.10) so that, on rearranging, we have

$$R_0 = \frac{E_0}{\alpha E_0 + \beta} \quad .. \quad .. \quad .. \quad .. \quad (6.11)$$

As before, the eggs obtained from any one of these R_0 groups of recruits are

$$E_0 = \gamma R_0 \quad .. \quad .. \quad .. \quad .. \quad (6.12)$$

From (6.11) and (6.12) we may obtain a general equation between the number of successive recruit broods and the corresponding egg-production. Thus for any year X the egg-production E_X can be written as

$$E_X = \gamma R_X$$

so that the number of recruits R_{X+1} surviving from the E_X eggs is

$$R_{X+1} = \frac{E_X}{\alpha E_X + \beta}$$

or

$$R_{X+1} = \frac{\gamma R_X}{\alpha\gamma R_X + \beta} = R_X\left(\frac{\alpha\gamma R_X + \beta + \gamma - \alpha\gamma R_X - \beta}{\alpha\gamma R_X + \beta}\right)$$

On rearranging, we find

$$R_{X+1} = R_X\left(1 - \frac{R_X - \dfrac{\gamma-\beta}{\alpha\gamma}}{\dfrac{1}{\alpha\gamma}\left(\alpha\gamma R_X + \beta\right)}\right)$$

It can be seen at once from this expression that if

$$R_X > \frac{\gamma - \beta}{\alpha\gamma}$$

then

$$R_{X+1} < R_X$$

and conversely. The population is therefore steady when

$$R = \frac{\gamma - \beta}{\alpha\gamma} \quad .. \quad .. \quad .. \quad .. \quad (6.13)$$

and if there is a transitory increase or decrease in the number of recruits in one year, the number in subsequent years will decrease or increase respectively until the steady state defined by (6.13) is regained. As far as transitory changes are concerned the population may therefore be regarded as a *self-compensating system* tending to regain its initial steady state.* With a maintained change in the egg-production per recruit we have a new coefficient γ' instead of γ and there will be a new stable value of R given by

$$R_0' = \frac{\gamma' - \beta}{\alpha\gamma'}$$

According to whether $\gamma' >$ or $< \gamma$, so will R_0' be $>$ or $< R$, and the population will steadily increase or decrease respectively until the new steady state is attained.

The mathematical form of the trends in egg-production and recruitment during the attainment of a steady state can be established without difficulty, and is relevant to the interpretation of data. By taking reciprocals of (6.10) we have

$$\frac{1}{R} = \alpha + \beta\left(\frac{1}{E}\right)$$

and, similarly,

$$\frac{1}{E} = \frac{1}{\gamma}\left(\frac{1}{R}\right)$$

If the steady state to which the population is tending is defined by E_∞, R_∞, these values can be used to establish a new origin, and we can write

$$\frac{1}{R'} = \frac{1}{R} - \frac{1}{R_\infty}, \quad \frac{1}{E'} = \frac{1}{E} - \frac{1}{E_\infty}$$

where R' and E' are measured with reference to the origin E_∞, R_∞. We then have

$$\frac{1}{R'} = \beta\left(\frac{1}{E'}\right), \quad \frac{1}{E'} = \frac{1}{\gamma}\left(\frac{1}{R'}\right)$$

so that there is a proportional relationship between the reciprocals of R' and E'. Suppose now that at time zero the population begins to approach a steady state with β and γ constant, following a disturbance which results in the initial values E_0', R_0'. By the same methods as used in connection with (6.2) and (6.3), it then follows that for the nth subsequent recruitment, i.e. for the value R_n' after n generations, we have

$$\frac{1}{R'_n} = \left(\frac{\beta}{\gamma}\right)^n \frac{1}{R_0'}$$

Transferring to the true origin, this equation becomes

$$\frac{1}{R_\infty} - \frac{1}{R_n} = \left(\frac{\beta}{\gamma}\right)^n \left(\frac{1}{R_\infty} - \frac{1}{R_0}\right)$$

Now from (6.13) we can write

$$\frac{1}{R_\infty} = \frac{\alpha\gamma}{\gamma - \beta}$$

and putting also†

---

*It may be noted that with (3.1) the effect of a *transitory* change is to cause the population to attain a new *permanent* level of abundance. To this extent the population described by (3.1) is therefore stable, but it is not a self-compensating system.

†As the word 'log' in this paper always refers to natural (base e) logarithms we omit the suffix 'e' throughout.

$$k = \log \frac{\gamma}{\beta}$$

we have

$$\frac{1}{R_\infty} - \frac{1}{R_n} = \left(\frac{\alpha\gamma}{\gamma - \beta} - \frac{1}{R_0}\right)e^{-kn} \quad .. \quad .. \quad .. \quad (6.14)$$

Thus the trend in recruitment is such that the difference between reciprocals of the value after n generations and the limiting value for the steady state decreases exponentially with the number of generations.

The behaviour of the population represented by (6.10) is shown diagramatically in Figs. 6.4, using the same conventions as in Figs. 6.1. Thus the initial steady state defined by values E_0 and R_0 is given by the point of intersection of the egg-production and recruitment curves, the former being indicated by the full line γ. Fig. 6.4.1 shows the behaviour following transitory increases and decreases in egg-production, the latter being displaced above or below the steady level E_0 to the values E_1 or E_2 respectively. The values of E and R during the transitional phase are plotted as a time-series at the bottom of the diagram. In Fig. 6.4.2 we suppose that a maintained decrease in egg-production per recruit occurs, the new egg-production curve being shown by the broken line γ'. The new steady state defined by the values R_0' and E_0' is given by the intersection of the line γ' and the recruitment curve and, as before, the transitional values of E and R are shown as a time-series below. Fig. 6.4.3. shows the behaviour following a maintained increase in egg-production per recruit.

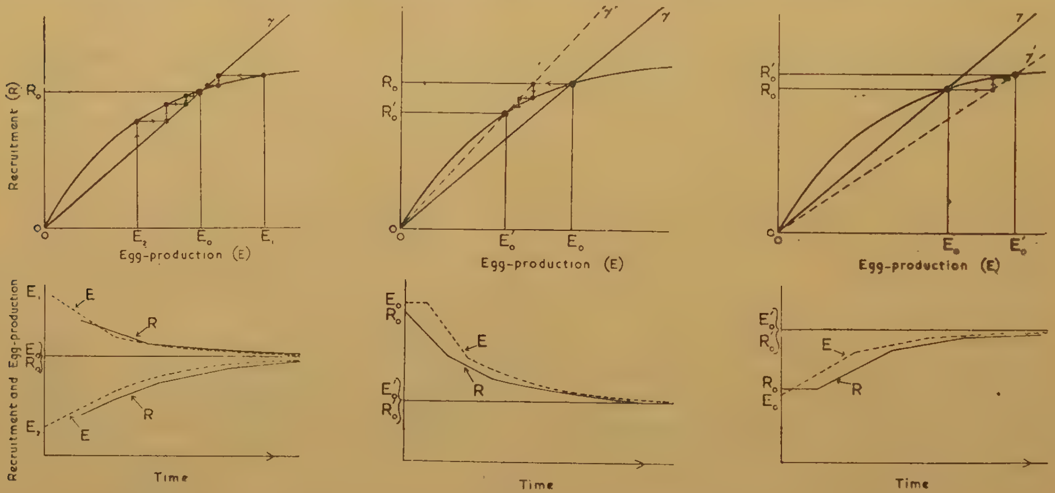

Fig. 6.4.1 Fig. 6.4.2 Fig. 6.4.3

FIGS. 6.4 THE DYNAMICS OF A SELF-REGENERATING MODEL WITH A LINEARLY DENSITY DEPENDENT LARVAL MORTALITY RATE (6·10)

[As in Figs. 6.1, the upper part of each diagram shows successive values of recruitment and egg-production following a change in egg-production per recruit of the adult population; in the lower part these are plotted as time series. With this form of larval mortality the population is 'self-compensating'; after a transitory change in egg-production per recruit (or in larval mortality) the original steady state is regained, while if the change is permanent a new steady state is reached. These properties should be contrasted with those shown in Figs. 6.1 and 6.6.]

Fig. 6.4.1 Recovery of stability following a transitory change in egg-production.

Fig. 6.4.2 Transition from one steady state to another following a sustained decrease in egg-production per recruit.

Fig. 6.4.3 Transition from one steady state to another following a sustained increase in egg-production per recruit.

In the above examples we have supposed that a change in egg-production is responsible for deflecting the population from its steady state but the conclusions remain the same if the recruitment is deflected by a change in the larval mortality rate. Thus if the latter change were maintained, the new steady state would be given by the intersection of the original egg-production curve with the new recruitment curve, and R_0' would be defined by (6.14) in which either or both the coefficients α and β were different. Further, it can be shown that a population in which there are a number of age-groups in the exploited phase reacts to either sustained or transitory changes in a manner essentially similar to the simple population considered above. With a sustained change the new equilibrium is approached more slowly than when only one age-group is present, and in the case of a transitory change the deflection from the normal state is less. The representation of mortality during early life given by (6.10) therefore produces a population behaviour which is in agreement with the general observations set out at the beginning of this section, and we shall use it in §6.1.3 to develop a model in which recruitment varies with population density.

6.1.1.2 *Some other possible mechanisms*

One important point which emerges from the above analysis is that a mortality which operates in a way such that its coefficient is independent of the density of the larvae cannot be directly responsible for *maintaining* the population in a steady state. This fact has, of course, been realised for some while and was first clearly stated by H. S. Smith (1935). In this category we must therefore put the mortality caused directly by unfavourable physical conditions of the environment and also certain of the effects of inter-specific predation, even though these factors may result in the μ_1 coefficients being very large. There are certain mechanisms, however, other than direct competition for food among the larvae themselves, which can contribute to the stability of the population, and which may incorporate the influence of the physical environment or predators.

Ricker and Foerster (1948) have put forward the interesting suggestion that when the larval density is low, individuals may grow more rapidly through a critical phase of their life than when the density is high. This involves a relationship between the food supply to the larvae and their mortality which differs to some extent from that postulated in §6.1.1.1. Let us suppose that the larvae while they are within a certain critical range of size are grazed by a predator; the extent of the mortality caused by the predator would therefore depend, *inter alia*, on the rate at which the larvae are able to grow through the critical range of size. For a simple treatment of this situation we may suppose that the predatory mortality can be denoted by a constant coefficient μ_1' and operates on the larvae from birth until they reach a certain size c at age t_c, after which they are too large to be eaten by the predator. The number surviving to this age is

$$N_c = Ee^{-\mu_1' t_c}$$

Between ages t_c and t_p we can suppose that other causes exert a mortality defined by the coefficient μ_2', where $\mu_2' < \mu_1'$. The number of recruits is therefore

$$R = Ee^{-\{(\mu_1' - \mu_2')t_c + \mu_2' t_p\}} \quad \dots \quad \dots \quad \dots \quad (6.15)$$

Now if there is competition for food among the larvae, even though it may not be sufficient to cause any direct mortality it will have some effect on the growth rate and hence on the age t_c at which the size c is reached. Hence t_c will be related in some way to the initial number of eggs E, and we must next see whether there is a simple relationship between these two quantities.

For reasons which are detailed in §9.4.1, we may represent changes in the rate of growth due to differences in the amount of food eaten by means of variations in the magnitude of the parameter W_∞ of the von Bertalanffy equation, and to the first approximation we may regard W_∞ as proportional to the food eaten by each larva and hence inversely proportional to the density of the latter. At low weights and over short periods of time we also find from the von Bertalanffy equation that t_c varies inversely with W_∞. Hence we have the relationships

$$t_c \propto \frac{1}{W_\infty} \propto \frac{1}{\text{food eaten}} \propto \text{density} \propto E$$

so that we might expect to find a roughly proportional relationship between egg-production and the age at which survivors reach the size beyond which they are free from the predatory effect. Making the substitutions

$$e^{-\mu_2' t_p} = \alpha'$$

and

$$(\mu_1' - \mu_2')t_c = \beta' E$$

in (6.15), where α' and β' are constants, we therefore have the expression

$$R = \alpha' E e^{-\beta' E} \quad .. \quad .. \quad .. \quad .. \quad (6.16)^*$$

A typical example of the form of the curve given by (6.16) is shown in Fig. 6.5, and it will be seen that it differs from the curves obtained from (6.10) in that for given values of α' and β' there is a certain egg-production which produces a *maximum* number of recruits.

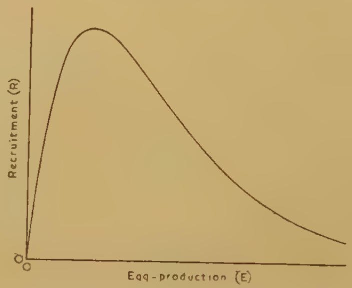

FIG. 6.5 A RELATIONSHIP BETWEEN EGG-PRODUCTION AND RECRUITMENT WHEN THE GROWTH RATE OF THE LARVAE IS DENSITY DEPENDENT (6.16)

[In this case a cause of larval mortality (e.g. predation) is assumed to operate while larvae are within a limited range of size. If growth of the larvae is density dependent, the time they take to grow through this critical range of size—and hence the severity of the mortality suffered by them—increases as their density increases. This results in the egg-recruit curve reaching a maximum and the population having the kind of dynamic properties shown in Figs. 6.6.]

We have not attempted a rigorous investigation of the stability of the population given by (6.16), but certain general conclusions can be drawn. Points on the curve to the *left* of the maximum define steady states similar to those given by (6.10) and illustrated in Figs. 6.4; a permanent change in egg-production per recruit, for example, causes the population steadily to approach the new steady state, provided this is still to the left of the maximum, while the system is self-compensating with respect to transitory changes. To the *right* of the maximum a new kind of behaviour appears. Thus while steady states are still theoretically possible, that is to say, a population could be set up with an appropriate egg-production per recruit which would remain in this state if undisturbed, the population may not be able on its own accord either to reach a steady state or maintain it despite fluuctations in the environment. The behaviour that will result is found to depend essentially on the relative slopes of the recruitment and egg-production curves in the region where the two cross, and the possible cases are illustrated in Figs. 6.6. In these diagrams the theoretical steady state is shown by the point of intersection of the recruitment and egg-production (γ) curves corresponding to the values R_0 and E_0 and we show the events following a change in the number of recruits to R_1.†

(i) If the slope of the recruitment curve is shallower than the egg-production curve in the region of intersection, the population will eventually reach a steady state, but during the transition phase it will oscillate with decreasing amplitude above and below the steady state, as shown in Fig. 6.6.1.

(ii) If the two slopes are about equal the population will be unable to reach a steady state and will undergo permanent oscillations of approximately constant amplitude. (Fig. 6.6.2.)

(iii) If the recruitment curve is steeper than the egg-production curve the population will again be unable to reach a steady state and the oscillations will be irregular and more violent than in case (ii). (Fig. 6.6.3.)

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*This is the 'compound exponential', $y = x^{a-bx}$ of Baas Becking (1946), who considers such expressions . . . "worthy of attention as their origin fulfils the biological demand of geometric multiplication with a restraining influence".

†From what has been said in §6.1.1.1 with reference to Figs. 6.4, the value R_1 can be regarded either as a temporary change or as defining a previous steady state.

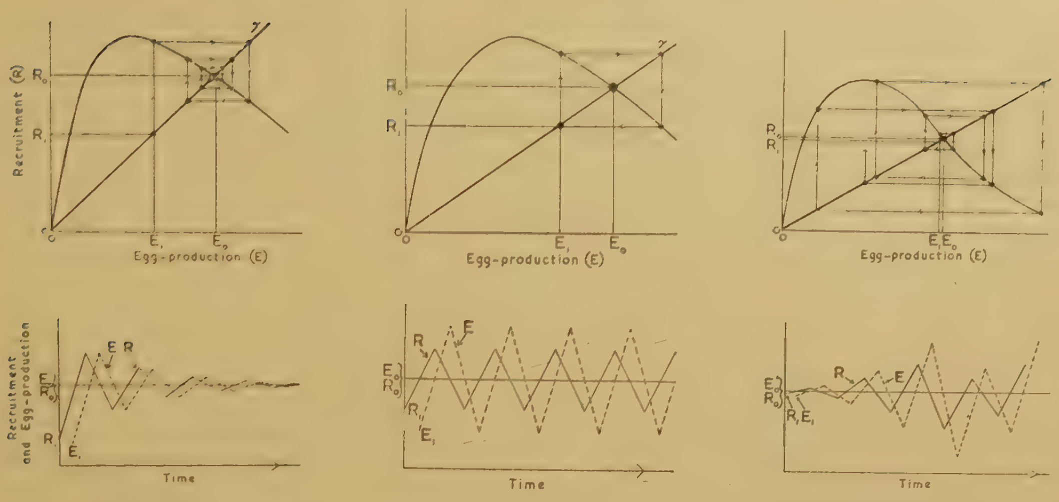

Fig. 6.6.1 Fig. 6.6.2 Fig. 6.6.3

FIGS. 6.6 THE DYNAMICS OF A SELF-REGENERATING MODEL WITH THE EGG-RECRUIT RELATIONSHIP DEFINED BY (6.16) AND SHOWN IN FIG. 6.5

[As in Figs. 6.1 and 6.4 the upper part of each diagram shows successive values of recruitment and egg-production following a disturbance from an initial steady state, while the lower part shows these changes plotted as time series. With steady states lying to the left of the maximum of the egg-recruit curve the dynamics are similar to those shown in Figs. 6.4. With steady states to the right of the maxima there is the possibility that permanent oscillations may follow even a transitory disturbance, depending on the relative slopes of the egg-production (γ) and recruitment curves in the region of their intersection.]

Fig. 6.6.1 Slope of recruitment curve shallower than that of egg-production curve at intersection. Recovery of initial steady state following a transitory disturbance.

Fig. 6.6.2 Slope of recruitment curve equal to that of egg-production curve at intersection. Permanent oscillations of equal amplitude following a transitory disturbance.

Fig. 6.6.3 Slope of recruitment curve steeper than that of egg-production curve at intersection. Permanent oscillations of increasing amplitude following a transitory disturbance.

In Fig. 6.6.3 it will be noted that the difference between R_0 and R_1 is very small and in practice the theoretical steady state could never be maintained even if the population could be set up with the values R_0 and E_0. With transitory changes the population is therefore self-compensating if the slope of the survival curve is shallower than that of the egg-production curve, but if it is the same or steeper, a transitory change will set up permanent oscillations. In either case the population will be unable to regain its previous steady state. The reaction of the population given by (6.16) to transitory or permanent changes in larval mortality or egg-production for steady states to the left of the maximum will therefore be the same as that given by (6.10), and in practice these are likely to be more usual than are steady states to the right of the maximum, especially in a heavily fished population where the egg-production per recruit is low. Furthermore, the maximum egg-production per recruit that can result from changes in fishing intensity is obtained when the latter is zero, i.e. in the virgin population, and even this may not be to the right of the maximum. On the other hand, a sufficiently high fishing intensity can reduce egg-production practically to zero, especially if the age at entry to the exploited phase is appreciably lower than the age at maturity.

In most cases we should therefore expect to find that the population behaviour given by (6.16) does not differ greatly from that given by (6.10), but the possibility that permanent oscillations may be set up is of considerable interest. Thus most investigations on the causes of fluctuations in natural populations have been concerned only with tracing their correlation with fluctuations in environmental factors; but the behaviour of (6.16) shows that a single change in environmental conditions, either transitory or sustained, may be sufficient to set up permanent self-induced oscillations in population abundance which would bear no obvious relation to subsequent environmental changes. These oscillations are not therefore of the same character as those given by the theoretical models of Volterra (1931), which are the result of the interaction between two populations; but recently there have been theoretical and practical studies dealing with oscillations within a single population which are of the same general type as those given by (6.16). Moran (1950) has investigated the properties of a theoretical population model in which the rate of change of numbers at any instant depends on the past history of the population, and showed that in these circumstances sustained cycles of oscillation could result. He termed this phenomenon *hysteresis*, and illustrated it with a diagram which is essentially the same as our Figs. 6.6. Nicholson (1950) has described a practical example of hysteresis in an experimental population of sheep blow-flies (*Lucilia cuprina*, Wien), in which the delayed effects of larval competition for food set up violent oscillations in the size of the population. In this connection, Palmgren (1949) has concluded, after a detailed study of the data on short-period cycles in northern mammal and bird populations summarised by Siivonen (1948), that these " . . . are largely explicable as a compound result of random variation . . . and the influence of the population density during the preceding year (auto-regression)". A cycle that may result from the action of a delayed density dependent factor (a term first used and defined by Varley, 1947) is illustrated by Lack (1951, Fig. 4B) by joining points for successive years in a graph of percentage winter mortality of the Bobwhite quail (Errington's (1945) data) against autumn population density. This method of presenting such data is of value also in the analysis of complementary fluctuations of fish abundance and fishing effort, that is, where the cycle is caused partially by predator-prey interaction.

There are interesting similarities between the properties of (6.10) and (6.16) and certain phenomena encountered in the study of simple one-stage servo-mechanisms. The property of self-compensation shown by (6.10) is analogous to the 'feed-back' process of a servo-mechanism, i.e. that process which tends to maintain a desired function by applying a compensating force depending on the extent to which the function actually being performed at any moment differs from the desired function. The population described by (6.16), on the other hand, can exhibit the property of 'over-shoot' in attempting to reach a theoretical steady state to the right of the maximum (e.g. Fig. 6.6.2); this is similar to the condition of excessive 'negative feed-back' in a servo-mechanism, though here it is due to the alternation of negative and positive feed-back.*

A further point of interest in connection with the above treatment is that it shows how factors which are not themselves influenced by the density of the population can nevertheless have an indirectly density dependent effect. For example, since growth is considerably influenced by temperature, the latter will be partly responsible for determining the length of time during which the larvae are exposed to predation. In fact, the coefficient β' of (6.16) would be expected to be approximately proportional to Q_1^{-t}, where t is the temperature in degrees centigrade and Q_1 is about 1.1 to 1.2. This suggests a possible way in which the physical environment can be partly responsible for a density dependent mortality, and what amounts to the same mechanism has in fact been postulated by Dickie (1950) to account for the observation that a good survival of the larvae of the scallop (*Pecten grandis*, Solander) is associated with high temperatures. He states that . . . "High temperature hastens their development to the settling stage, thereby reducing their time of exposure to enemies and other hazards". Further examples of this kind are discussed by Solomon (1949).

A particularly interesting relationship between egg-production and recruitment is that in the Georges Bank haddock, described by Herrington (1948) and reproduced here in Fig. 6.7 (circles). The data are, admittedly, rather scattered (though no more than is usual in such cases) but they give a decided impression of a maximum recruitment occurring at a certain intermediate level of egg-production. To this extent the relationship would appear to be of the kind given by (6.16), but the decline in recruitment at higher egg-productions is so sharp that a curve describing the data would seem to be nearly symmetrical about its maximum; this suggests that some more intense interaction may be involved than that of the kind from which (6.16) was developed. Herrington found that when adults were abundant they spread into the nursery grounds to a greater extent than usual. He noticed further that plotting adult density against the estimated contemporary abundance of one-year old fish (i.e. the progeny from the previous year's spawning) also produced a curve with a maximum at an intermediate level of adult density. These observations led him to suggest that when adults were abundant they competed directly with the young for food, the resulting shortage of food for the latter being a direct cause of their mortality.

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*For an interesting and relevant account of the properties of self-compensating and oscillating systems we would refer the reader to Wiener (1948) and Farrington (1951). Recently, there has been considerable discussion among biologists, reviewed by Wisdom (1951), of the Ashby-Wiener cybernetic hypothesis that feed-back is an important feature of biological processes, though most attention has been paid to neurological applications. In fact, many problems concerning the exploitation of natural populations can usefully be considered in terms of servo-communication theory.

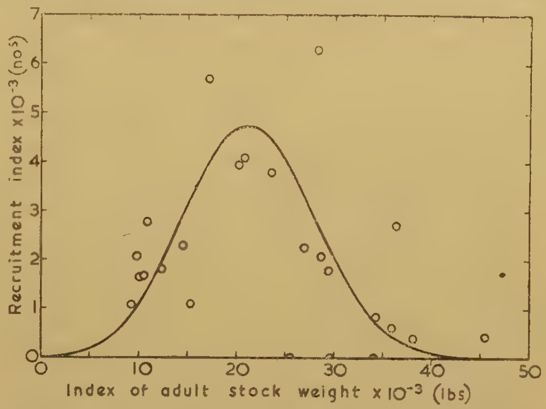

FIG. 6.7 EGG-PRODUCTION AND RECRUITMENT IN GEORGES BANK HADDOCK

[Relationship between weight-density of adult stock and recruitment; data from Herrington (1948). The curve is obtained from (6.17 with $\alpha' = 0.0072$, $\beta_0' = -0.373$, $\beta_1' = 0.0099$.]

There are, however, certain difficulties in accepting this explanation. Owing to the marked serial dependence between adult density in successive years (see §6.2 and Herrington, 1948, Table III), if there was any particular relationship between adult density and true recruitment there would also be a not dissimilar one if the adult densities were displaced by one year—as is done by plotting adults against one-year fish. This particular line of evidence therefore neither proves nor, of course, disproves the hypothesis of interaction between adults and one-year old fish. Again, there is evidence from other species (see §9.4.1) to suggest that when once the pelagic larval stage is passed, fish are remarkably resistant to shortage of food and seem unharmed by a food supply much below that for normal growth. If shortage of food for the young haddock was indeed severe enough drastically to increase their mortality it would be expected that the growth of some at least of the survivors would be adversely affected, and Herrington does not show that this has happened.

Something of the difficulty of explaining the Georges Bank haddock phenomenon other than by the mechanism of (6.16) can be gauged by comparison with other circumstances in which it has been established that a decreased number of survivors is obtained above a certain level of egg-production. One is when the space in which the eggs are laid is extremely limited, and is exemplified by the investigations of McKenzie (1947) on the effects of crowding of smelt eggs on the production of larvae. By restricting the area of the spawning beds it was possible to increase the egg-density to such an extent that . . . "not merely a smaller proportion but smaller total numbers of larvae hatch out successfully". The other is when the family, rather than the whole population, is the competing unit, which also has the effect of making competition among young particularly severe when conditions are unfavourable. Thus Lack (1948b), using data of Wright and Eaton (1929) for the guinea pig, has shown that with increasing litter size there is first an increase and then a decrease in the number of survivors. But neither of these circumstances are found in marine fish populations; thus although it could be postulated that larval mortality rate increases with larval density more rapidly than the linear relationship used above, it is not easy to see how this could happen in a marine species where larvae are unlikely to be so crowded that they are prone, through intra-specific causes, to a mortality approaching an 'epidemic' in its severity.

It does therefore seem that adults may be in some way involved, in order to account for the greatly increased mortality of young when adults are abundant, but possibly in a way different from that suggested by Herrington. As an example of the kind of mechanism that could produce an $E - R$ relationship such as that in the Georges Bank haddock, we can suppose that the external predation postulated to develop (6.16) is, in fact, due to the adults themselves. If adults only feed on young while the latter are within a certain range of size the model formulated by (6.15) is applicable but with the coefficient μ_1' roughly proportional to adult abundance, and hence to egg-production E. Assuming also that growth of the young at this stage varies inversely with their own density, so that t_c can be taken as roughly proportional to E as before, we obtain the relationship

$$R = \alpha' E e^{-(\beta_0' E + \beta_1' E^2)} \quad \text{.. .. .. ..} \quad (6.17)$$

With suitable values of β_0' and β_1' this equation can produce a curve nearly symmetrical about the maximum value of R. Fig. 6.7 shows an example that gives an adequate representation of Herrington's adult stock and recruitment data (1948, Table III), with coefficients $\alpha' = 0.0072$, $\beta_0' = -0.373$, $\beta_1' = 0.0099$, this does not, of course, establish the mechanism as being the true one. Indeed, haddock are not often found to have been feeding on young fish, although A. B. Needler (1931) records instances of this, and they have a decided liking for herring spawn. Nevertheless, this example gives some idea of the kind of mechanism needed to produce a symmetrical $E - R$ curve, and further studies on larval mortality in the Georges Bank haddock should contribute much to our understanding of this obscure but important phase of the life-history.

From this brief survey of possible relationships between egg-production and the number of subsequent recruits, it would seem that they can be divided into two categories according to whether the curve is asymptotic or has a maximum. Such data as exist suggest that the asymptotic curve is the more common (see §15.2.3.2), though it is clear that insufficient is known to establish such a conclusion with any certainty. Nevertheless, it is supported indirectly by two conclusions which follow from the theoretical discussion given above. First is the fact that all the mechanisms considered require the larval mortality rate to be dependent on larval density, but whereas this alone is sufficient to produce an asymptotic curve certain additional factors, which may not be so generally present, are needed to produce a maximum in the $E - R$ curve. Second, is the finding that in curves having a maximum, stability is possible only to the left of the maximum, though, of course, the actual magnitude of any oscillations of this type depends on the number of age-groups comprising the population. Bearing all these considerations in mind, we believe that an asymptotic curve is probably the most generally useful method at the present time of representing the relationship between egg-production and recruitment, and in this paper we shall therefore use (6.10) in theoretical models that take this relationship into account.

Ricker (1954a, b) has, however, concluded that the 'reproductive curve' for fish is, most typically, not asymptotic but dome-shaped, the right-hand limb sometimes sloping downward only slightly, sometimes quite steeply. He develops a compound exponential expression of the same form as (6.16), but from assumptions involving cannibalism or other compensatory density dependent predation, and uses this to fit to the data available to him. Although the fit to data referring to some invertebrate populations under experimental conditions is satisfactory, this is not necessarily evidence in favour of its general applicability, because some at least of the factors responsible for the rather steep descent of the right-hand limb of experimental curves (e.g. close proximity of adults and young, fouling of the medium) are often lacking under natural conditions. It must be admitted, moreover, that the variability in the case of the examples of wild fish stocks is usually so great that the true form of the curve—and in particular whether it is asymptotic or peaked—cannot readily be distinguished, and the significance of determined values of parameters is not tested. In this connection it must be remembered that a markedly dome-shaped curve will usually give a better fit to any set of widely scattered data than an asymptotic one. Nevertheless, in all the cases examined the curves of *best* fit had maxima to the left of the 45° line, giving the possibility of oscillations, as mentioned above. Now although in our view the general occurrence of a peak recruitment at some intermediate size of spawning stock is not yet clearly established, Ricker's general conclusions concerning the significance of density dependent mortality among young fish in relation to the stability of fish stocks, the possibility of self-induced oscillations under certain conditions, and the effects of exploitation and of random fluctuations in reproductive success on abundance trends and variation, are all in broad agreement with our own. He has listed some possible kinds of compensatory mortality, including the one which we had believed likely to be the most generally important, namely that arising from severe competition among young fish for food. He also considers briefly the possibility of reduced effectiveness of reproduction at very *low* population densities. It is to be hoped that in the future more adequate data for major fish stocks will become available, so that these most important problems can be thoroughly investigated and some firm statements made concerning the main regulatory factors.

6.1.2 *Annual egg-production of a fish population*

We now turn to the second aspect of the problem of developing a self-regenerating population model, namely that of obtaining an expression for the fertile egg-production of a fish population in terms of its age- and size-structure and abundance.

Volterra (1938) has shown that under certain conditions of random mating, with a constant sex-ratio, the 'birth-rate' would be expected to be proportional to the square of the number density of the adult population. This may well be the case in, say, a lobster population of the type described by Poulsen (1946) where copulation occurs; here, a scarcity of males, caused by the differential action on the sexes (favouring females) of the Danish size-limit and the low survival of rejected 'smalls', is a factor which can reduce the size of a brood. It can be shown, however, that if there is free liberation of gametes, with spermatozoa greatly in excess of eggs, and especially if the percentage of successful fertilisations is fairly high, then the number of fertilised eggs would tend to be a constant fraction of the numbers laid. In addition, a large spawning population would tend to distribute eggs over a rather wider area than a small one, so that the number of gametes per unit volume, which in such a situation determines the rate of fertilisation, would not be expected to change much.

As far as can be judged at the present time it is these latter conditions that represent most nearly the events during the spawning of the majority of marine fish. For example, the work of Simpson (1951a, p. 13) on the fecundity and spawning of plaice in the southern North Sea has shown that the proportion of unfertilised plaice eggs is extremely small, as is also the number of eggs left to be resorbed in the ovary when spawning is complete. Further evidence in this species comes from the fact that the local density of males on the spawning grounds appears to be several times that of females, and that each male extrudes spermatozoa during most of the spawning season; these features suggest that within a wide range of population abundance there is likely to be, at any time, an excess of spermatozoa. For our present purposes we shall therefore disregard the contribution of males to reproduction, and assume that the latter is limited by egg-production only. Any further discrepancy that there may be between the number of eggs laid and the number of larvae hatched, i.e. as a result of egg mortality, can of course be taken into account by assigning an appropriate value to ${}_1\mu_1$ in the differential equation from which (6.10) is derived (see §6.1.1.1), and putting ${}_1\mu_2$ to zero.

Since eggs are produced from the germinal epithelium, it might be expected that the number produced by a fish during a spawning season would be roughly proportional to the area of that epithelium. Now, if the ovary was a simple bag growing isometrically with the rest of the body, and provided also that the size of the eggs did not vary with that of the fish, fecundity would then be proportional to the two-thirds power of the body weight. Although constancy of egg size seems to be a feature of marine as opposed to freshwater fish (see e.g. Simpson, 1951b), usually the germinal epithelium is so highly convoluted that it completely fills the ovary: in such cases fecundity would be expected to be proportional to body weight itself. A close approximation to this has indeed been found by Raitt (1933) for haddock and Simpson (1951a) for plaice, in both of which species the eggs are small and fill the whole volume of the ovary. How widely applicable this rule is among marine fish cannot be stated at the present time, since there do appear to be certain exceptions to it.* It is clear, however, that the egg-production of either a haddock or a plaice population can be taken as approximately proportional to the total weight of the mature females in it. This will be taken as the central relationship in the following theory, but it will be seen that the necessary modifications could easily be made if it were found in another case that fecundity was proportional to a power of weight other than one.

We shall denote the fecundity per gm. weight of females by the coefficient χ, and assume that the mortality and growth coefficients are the same for both sexes, so that the proportion of females at any age can be denoted by a constant, s. The remaining factor requiring definition is the age at first maturity, which we shall call t_η. Where the onset of maturity is spread over a range of age, t_η can be defined approximately as the age at which 50% of the females are mature.

The annual egg-production of the population is given by

$$E = s\chi_\eta \bar{P}_W$$

where ${}_\eta\bar{P}_W$ is the annual biomass of the mature section of the population. Two cases can arise, depending on whether the age t_η is higher or lower than the age $t_{\rho'}$ at which the fish first become liable to capture. Thus, when $t_\rho \leqslant t_\eta < t_{\rho'}$, we have by the methods of §5,

$$E = s\chi R W_\infty e^{-M(t_\eta - t_\rho)} \sum_{n=0}^{3} \Omega_n e^{-nK(t_\eta - t_0)} \left\{ \frac{1 - e^{-(M+nK)(t_{\rho'} - t_\eta)}}{M + nK} + \right.$$
$$\left. + \frac{e^{-(M+nK)(t_{\rho'} - t_\eta)}}{F + M + nK} \left(1 - e^{-(F+M+nK)\lambda}\right) \right\} \quad .. \quad (6.18)$$

and when $t_{\rho'} \leqslant t_\eta < t_\lambda$, we have

$$E = s\chi R' W_\infty e^{-(F+M)(t_\eta - t_{\rho'})} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_\eta - t_0)}}{F + M + nK} \left(1 - e^{-(F+M+nK)(t_\lambda - t_\eta)}\right) \quad .. \quad (6.19)$$

There is evidence (e.g. Wallace, 1909; Arora, 1951) to suggest that the onset of maturity may be conditioned more by the weight of the fish than by its age, so that if we have to deal with variations in growth rate, t_η will no longer be a constant. In such a case we can define by W_η the weight of a fish at first maturity, or at which 50% of the individuals first reach maturity, and it is given from (3.7) by

$$W_\eta = W_\infty(1 - e^{-K(t_\eta - t_0)^3})$$

from which

$$t_\eta = t_0 - \frac{1}{K} \log \left\{ 1 - \left(\frac{W_\eta}{W_\infty} \right)^{1/3} \right\}$$

This expression for t_η may be substituted in either of the above equations. Certain other complications may require consideration, and can easily be dealt with by modifications of the above methods. For example, the mortality and growth coefficients of females may differ appreciably from those of males, and in this case we can put

$$E = \chi_\eta \bar{P}^{♀}_W$$

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*On theoretical grounds, departures from a proportional relationship between fecundity and weight would be expected if the germinal epithelium was not sufficiently convoluted to fill the ovary, if the latter grew anisometrically with the rest of the body, or if egg size varied with ovary size. As mentioned above, egg size within most marine fish seems remarkably constant, though the instance of a departure from a proportional fecundity-weight relationship through variation in egg size in a marine fish appears to be provided by the work of Hagerman (1952) on the Pacific Dover sole (*Microstomus pacificus* Lockington). In freshwater fish, however, variation in egg size can be considerable: whether this is the cause of the linear relationship between fecundity and length claimed by Allen (1951) for New Zealand trout is not clear, but it may well result in the variation of fecundity with size being less consistent than in marine fish. A further complication is that the survival of fry hatched from large eggs may be better than from small ones (see, e.g., Svärdson, 1949 and Rodd, 1946); if this happened, it would tend to offset the departure from a proportional relationship between fecundity and weight caused by variation in egg size.

where ${}_{\eta}\bar{P}_{W}^{\female}$ is the mean annual biomass of the mature females of the population. E is therefore given by equations of the same kind as (6.18) and (6.19) above, but which do not contain the sex-ratio and in which all parameters refer specifically to female fish.

In some cases it may be desirable to use summation methods to evaluate E, for example if past age-composition data with large fluctuations in recruitment are to be analysed, and we may proceed as follows. Denoting by s_0, s_1, s_2, etc. the proportion of females in each age-group at spawning time, that is at ages t_η, $t_\eta + 1$, $t_\eta + 2$, etc., and by p_0, p_1, p_2, etc. the proportion of these females which are mature, the total number of mature females present on the date of spawning, τ_η, can then be written as

$$N_{\tau_\eta}^{\female} = p_0 s_0 N_{t_\eta} + p_1 s_1 N_{t_\eta + 1} + p_2 s_2 N_{t_\eta + 2} + \ldots\text{.etc.}$$

To express this summation in terms of recruitment and mortality we suppose, for simplicity, that the date on which fish reach age t_λ coincides with date τ_η,* and that $t_\rho \leqslant t_\eta < t_{\rho'}$.

Then putting

$$\left.\begin{aligned} t_{\rho'} - t_\eta &= H + h \\ \text{and} \qquad & \\ t_\lambda - t_{\rho'} &= J + j \end{aligned}\right\} \begin{array}{l}\text{where } H \text{ and } J \text{ are integral} \\ \text{numbers of years, and } h \text{ and} \\ j \text{ are fractions of a year}\end{array}$$

and summing gives

$$N_{\tau_\eta}^{\female} = R\left[e^{-M(t_\eta - t_\rho)} \sum_{r=0}^{H} s_r p_r e^{-Mr} + e^{-M\rho - (F+M)(1-h)} \sum_{r=H+1}^{H+J+1} s_r p_r e^{-(F+M)(r-H-1)}\right]$$

We have previously assumed that the number of eggs laid at a spawning season per gram weight of fish (i.e. the coefficient χ), is a constant, but if the data make it necessary, χ can easily be made to vary with age when summation methods are being used.† The total number of eggs laid during a spawning season by the population can be written as

$$E = \sum p_r s_r \chi_r \,.\, w_{t_\eta + r} \,.\, N_{t_\eta + r} \qquad \ldots \quad \ldots \quad \ldots \quad (6.20)$$

where $w_{t_\eta + r}$ is the weight of a fish at age $t_\eta + r$, and χ_r has a value appropriate to fish of that age. Since, from (3.7),

$$w_{t_\eta + r} = W_\infty (1 - e^{-K(t_\eta + r - t_0)})^3$$

substitution in (6.20) gives

$$E = RW_\infty\left[e^{-M(t_\eta - t_\rho)} \sum_{r=0}^{H} s_r p_r \chi_r \,.\, e^{-Mr}\left(1 - e^{-K(t_\eta + r - t_0)}\right)^3 + \right.$$
$$\left. + e^{-M\rho - (F+M)(1-h)} \sum_{r=H+1}^{H+J+1} s_r p_r \chi_r \,.\, e^{-(F+M)(r-H-1)}\left(1 - e^{-K(t_\eta + r - t_0)}\right)^3\right] \quad \ldots \ (6.21)$$

It will be noted that if $t_\eta \geqslant t_{\rho'}$, the first term of this equation disappears.

6.1.3 *A self-regenerating‡ population model*

These representations of pre-recruit mortality and population fecundity may readily be introduced into the simple population models of Part I. If any of the equations for E

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*It will be remembered that the value of t_λ is to some extent arbitrary, and that it will usually be large. Adjustment of its value by a fraction of a year will therefore have no significant effect on the value of $N_{\tau_\eta}^{\female}$.

†The data of Raitt (1933) for the North Sea haddock, is used in this way in §15.2.3.2.

‡According to Wilbur (1941) this term is used by radio-engineers to describe a system which "feeds back into itself".

developed in §6.1.2 above are divided by R, we have an expression giving the annual number of eggs laid per recruit which we have previously denoted by γ. We can therefore write

$$E = \gamma R$$

and putting this expression for E in (6.10) gives

$$R = \frac{1}{\alpha}\left(1 - \frac{\beta}{\gamma}\right) \quad \ldots \quad \ldots \quad \ldots \quad (6.22)$$

which may be substituted in any of the equations for Y_W, $\bar{P}_W$, etc. of Part I. For example, from (4.2) and (6.22) we have the mean annual yield from the population given by

$$Y_W = \frac{FW_\infty e^{-M\rho}}{\alpha}\left(1 - \frac{\beta}{\gamma}\right) \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F+M+nK)\lambda}\right) \quad \ldots \quad (6.23)$$

which may be regarded as a 'self-regenerating' form of (4.4), with the annual number of recruits dependent on the characteristics of the adult population of which they are the progeny.

6.1.4 *Note on the effect of the entry of recruits into several age-groups*

The final point to consider is the introduction of the dependence of recruitment on the population density in the case in which recruits enter into several age-groups.

If we define by $R_{1\rho}$ the total number of fish in a given brood surviving to an age just less than ${}_1t_\rho$—that is, the age at which the first sub-group ${}_1R$ enters the exploited area—and assume that the pre-recruit mortality coefficients μ_2 for all fish greater than this age are small enough to be disregarded, then it follows that the number in any sub-group bears a constant relationship to the number $R_{1\rho}$, and hence to the total number of recruits, R, which eventually enter the population from that brood. This assumption will not give rise to any serious difficulties provided that the age ${}_1t_\rho$ is high enough for fish to have passed the larval stages in which their mortality might be appreciably affected by factors such as local aggregations of food.*

Now, by defining the coefficients α and β as effective up to age ${}_1t_\rho$, we can write

$$R_{1\rho} = \frac{E}{\alpha E + \beta} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.24)$$

and with the above assumption we also have

$${}_rR = {}_rcR_{1\rho} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.25)$$

where ${}_rc$ is a constant denoting the proportion that the sub-group ${}_rR$ is of the total number in the brood surviving to age ${}_1t_\rho$. Following the procedure of §6.1.3, we can write

$$E = \sum_{r=1}^{\Phi} {}_rR_r\gamma \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.26)$$

where Φ denotes the total number of sub-groups and ${}_r\gamma$ is the number of eggs per recruit laid annually by fish originating from the sub-group ${}_rR$. Substituting for ${}_rR$ from (6.25) gives

$$E = R_{1\rho} \sum_{r=1}^{\Phi} {}_rc_r\gamma \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.27)$$

---

*${}_1t_\rho$ in North Sea plaice, for example, is about 2.4 years (§15.1.3).

and eliminating E from (6.24) and (6.27) gives

$$R_{1\rho} = \frac{1}{\alpha}\left(1 - \frac{\beta}{\sum_{r=1}^{\Phi} {}_r c_r \gamma}\right)$$

so that, from (6.25)

$$ {}_r R = \frac{{}_r c}{\alpha}\left(1 - \frac{\beta}{\sum_{r=1}^{\Phi} {}_r c_r \gamma}\right) \qquad \ldots \quad \ldots \quad \ldots \quad (6.28)$$

This expression for ${}_rR$ may be substituted in any of the equations developed in §9.3 in which other characteristics of the fish comprising each sub-group are incorporated.

6.2 YEAR-TO-YEAR VARIATIONS IN THE TOTAL NUMBER OF RECRUITS

In the expressions developed in §6.1.1 to relate the number of recruits to the number of eggs of which they are the progeny, the derived larval mortality coefficients [e.g. α and β of (6.10)] are treated as constants. Hence the models are deterministic in that they require that in a given population a certain number of eggs will always give rise to the same number of recruits. Now, it is characteristic of fish populations that the number of recruits varies greatly from year to year, even though egg-production may remain at a roughly constant level, and an important cause is variation in the pre-recruit mortality rate, especially during the early larval stages. This could be represented in a theoretical model by appropriate changes in coefficients such as $\mu_1(t)$ and $\mu_2(t)$ of (6.8). At the present time, however, it is scarcely possible to deduce the magnitudes of such parameters that would apply to a given set of environmental conditions (see §15.2.3), and discussion here will be restricted to establishing the effect of a varying recruitment on certain kinds of assessments needed for fishery regulation, without attempting to analyse the causes of that variation.

The most useful case to consider is that of a fishery in which the fishing intensity has become stabilised—either naturally or through regulation—and the annual yield is fluctuating about a constant mean as a result primarily of year-to-year variations in recruitment. To set up a theoretical model of such a population we therefore assume that factors other than recruitment can be represented by constant parameters, as in the simple models of Part I, and evaluate the yield from the whole population during the course of a single year, as in §4.2, instead of from any one of its constituent broods fished throughout its fishable life-span. For simplicity, we measure the annual yield from the date $\tau_{\rho'}$ on which fish become liable to capture, and suppose that we are dealing with a fishery in which recruits enter into a single age-group only.

If we denote the number of recruits which first become liable to capture in a given year X by R_X, and in the previous year $X - 1$ by R_{X-1}, etc., then the yield from the whole population during the year X is given, from §4.2, by the equation

$${}_XY_W = FW_\infty e^{-M\rho} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F+M+nK)}\right) \sum_{z=0}^{\lambda-1} R_{X-z} \,.\, e^{-(F+M+nK)z}$$

which is analogous to that deduced by Doi (1951) as far as the treatment of fluctuating recruitment is concerned. In general, the yield during the year $X + p$ is

$${}_{X+p}Y_W = FW_\infty e^{-M\rho} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F+M+nK)}\right) \times$$

$$\times \sum_{z=0}^{\lambda-1} R_{X+p-z} \,.\, e^{-(F+M+nK)z}$$

The *mean yield*, over a period of q years, is therefore

$$ {}_q\bar{Y}_W = FW_\infty e^{-M\rho}\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\left(1-e^{-(F+M+nK)}\right)\sum_{z=0}^{\lambda-1}e^{-(F+M+nK)z}\sum_{p=0}^{q-1}\frac{R_{X+p-z}}{q} \quad \ldots \quad (6.29) $$

If there is no trend in the year-to-year variations in R over the period of q years, then as q increases

$$ \sum_{p=0}^{q-1}\frac{R_{X+p-z}}{q} \rightarrow \text{constant} $$

for all values of z, this constant being $\bar{R}$, the mean of the distribution of R. Consequently, (6.29) may be re-written

$$ \overset{q\to\infty}{{}_q\bar{Y}_W} = F\bar{R}e^{-M\rho}W_\infty\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\left(1-e^{-(F+M+nK)\lambda}\right) \quad \ldots \quad (6.30) $$

Now we may say that whatever the distribution of R, the values of $\bar{R}$ relating to a series of finite periods of time will be distributed approximately normally; in these circumstances, therefore, we reach the important conclusion that the most probable mean annual yield over a given finite period of time can be calculated from (4.4) in which the symbol 'R' is understood to be the mean annual recruit numbers during that time.

Another important requirement is to express the effect of variation in recruitment on the variation of the annual yield, since a prediction of the expected variation in yield after regulation, as well as its most probable mean level, must be the basis of any objective method of testing whether the effect of regulation is within the expected limits (see §19.2.3). For this purpose we continue to assume for the moment that the whole of the variation in yield is due to that of recruitment, and also that recruits enter into one age-group only. If successive recruitments are independent, we can then write

$$ \sigma_y^2 = \sigma_R^2\,(u_1^2 + u_2^2 + \ldots\text{etc.}\ldots u_\lambda^2) = \sigma^2\sum_{\theta=1}^{\lambda}u_\theta^2 \quad \ldots \quad \ldots \quad (6.31) $$

where σ_y^2 and σ_R^2 denote the true variances of yield and recruitment, and the weighting coefficients u_1, u_2, ... etc., denote the yield per recruit obtained from each age-group of the exploited phase. An expression for these weighting coefficients can be deduced by the methods of §4.2; thus for the $(\theta + 1)$th year of life in the exploited phase we have

$$ u_{\theta+1} = FW_\infty e^{-(F+M)\theta-M\rho}\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}+\theta-t_0)}}{F+M+nK}\left(1-e^{-(F+M+nK)}\right) \quad \ldots \quad (6.32) $$

Now, the two assumptions involved in (6.31), namely that successive recruitments are independent and that all parameters other than recruitment are constant, are not likely to be exactly true in practice. If recruitment was not near an asymptotic limit (see §6.1.1), a positive correlation between successive recruit numbers could arise as a result of, say, a very large year-class increasing the abundance of the mature stock and hence the value of E for several successive years, and conversely; or possibly through a tendency for certain environmental conditions to vary with a periodicity greater than one year. This would result in the variance of yield predicted from (6.31) being an underestimate of the true variance. The direction of the effect on the variance of yield of variation in parameters other than recruitment is less easy to anticipate, since according to whether the changes are in the same or opposite direction as the changes in yield, so will the true variance of yield be greater or smaller than would be computed from (6.31). This problem is discussed further in §15.2.2, where it is pointed out that both kinds of changes will usually occur together, so that if both are small, the effect on the variation of yield will be smaller still. Clearly, if there were large variations in a factor such as fishing intensity, it would be necessary to take this fact into account when developing an expression for the variance of yield; but there will be many cases where although the variation in factors other than recruitment is not as great as this, yet an assumption of constancy is not sufficient. In these circumstances most of the error that would result from the use of (6.31) can be avoided by specifying a residual yield-variance term, ${}_x\sigma_y{}^2$, and modifying (6.31) to become

$$\sigma_y{}^2 = \sigma_R{}^2 \sum_{\theta=1}^{\lambda} u_\theta{}^2 + {}_x\sigma_y{}^2 \quad \ldots \quad \ldots \quad \ldots \quad (6.33)$$

An estimate of ${}_x\sigma_y{}^2$ can be obtained by comparing an observed variance of yield with that predicted from the variance of recruitment during the same period, as described in §15.2.2.

It will be noted from (6.33) that the effect of variations in recruitment on the variations in yield will be damped to an extent depending on the number of age-groups in the exploited phase and on how rapidly the proportion of the total yield which is obtained from successive age-groups decreases with age. If recruitment occurs in several age-groups instead of one, the effective recruitment in any one year, denoted by R_X, will itself have a smaller variation than that of the size of the individual recruit broods, R. The relationship between the variation of R and of R_X will be of the same form as (6.31), and with the terminology of §6.1.4 we denote by p_r the proportion which the rth recruit sub-group is of the total year-class when it has been recruited. Thus we have

$$\sigma_{R_X} = \sigma_R \sqrt{\sum_{r=1}^{\Phi} p_r{}^2} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (6.34)$$

When there is recruitment into more than one age-group, the effective recruitment R_X may be substituted in place of the true recruitment R in the above expressions. It should be noted, however, that even though successive values of R may be independent, those of R_X will be positively correlated since any one recruit brood makes some contribution to two or more adjacent values of R_X. When predicting the variation of yield in such cases it is therefore preferable to use (6.33) so that the effect of the auto-correlation of successive R_X values can be included in the residual variance term ${}_x\sigma_y{}^2$.

It should be mentioned, finally, that the variances referred to above (denoted by the symbol σ) are specifically the true variances, and not those that would be estimated from data. The latter, whether of yield or recruitment, are liable to bias as well as random sampling error, the elimination of which is discussed in §15.2.2.

SECTION 7: NATURAL MORTALITY

7.1 Causes of Natural Death in Fish

As we mentioned in §3.2, the theoretical treatment of natural mortality in fish populations presents certain difficulties, these being due largely to the scarcity of information relating to the causes of natural death in adult marine fish. Predation is perhaps the most general 'external' cause, and the evidence has been reviewed by Errington (1946). The majority of recorded instances of predation refer to lake or river fish, but even here, direct evidence and measurement of the effect on the prey population seem relatively rare. Perhaps the most striking example in commercial fisheries is that of the predatory activity of the sea-lamprey (*Petromyzon marinus*) on certain fishes of the Great Lakes, discussed by Applegate (1951) (see also §9.4.3.2.4). Again, according to White (1939)—quoted by Huntsman (1948)—fish-eating birds are sometimes a major cause of mortality in salmon, and their removal results in an increase in the salmon population. Among other causes may be mentioned the low temperatures in the North Sea in 1929 (Lumby and Atkinson, 1929) and again in 1947 (Simpson, 1953), which was responsible for the death of large numbers of demersal fish,* and the poisonous effect of the dinoflagellate *Gymnodinium brevis* in the waters off the west coast of Florida (Gunter, 1949). It would seem that the latter is spasmodic in its occurrence, but it is possible that low winter temperatures in the North Sea are a regular component of the natural hazard in certain species, though to a much lesser extent than in the abnormally severe years mentioned above. Something like this situation was also found in Michigan lakes studied by Beckman (1950), who has used the reductions in population abundance during prolonged winters as an opportunity for investigating the relationship between growth and density (see §9.4).

Vaughan (1934) says that epidemic disease is an important cause of mortality in some marine fish. We have no evidence that this is so in the North Sea, but the possibility remains. If it does occur, the mortality caused is most unlikely to be constant in magnitude, though some parasites could have a stable effect.† Nevertheless, as we shall show in Part IV, the characteristics of the natural mortality rate have a particularly important bearing on the reaction of a population to exploitation and hence on the problem of fishery regulation. It is therefore of value to consider some of the theoretical implications of analysing this factor in more detail than has been done in Part I. Thus the population models developed in §7.2, in which the natural mortality coefficient varies with the population density, are used in §§18.2 and 18.5.1 to make some appreciation of the probable importance of this relationship in the case of the North Sea plaice, even though no direct data are available. For the above reasons the methods discussed in this section are largely empirical, though the case where natural mortality in an exploited population is due to predation is considered from an analytical standpoint in §11.2.2.

7.2 VARIATION OF THE NATURAL MORTALITY COEFFICIENT M WITH AGE

7.2.1 *Trends in natural mortality*

So far we have taken the natural mortality coefficient M to be constant between ages t_ρ and t_λ, after which it becomes infinite, so that t_λ is the maximum age which a fish can attain. When the possible causes of natural death in fishes are considered in more detail, however, it can be seen that these might well result in a trend with age in the magnitude of the natural mortality coefficient. For example, as fish grow old they may become senile and hence more susceptible to predation, disease, or to unfavourable environmental conditions in general; also the physiological demands of spawning may become progressively greater with increasing age. All such factors would tend to increase the natural mortality rate with age, but if there are intrinsic differences in susceptibility to them among individuals comprising each year-class when it is recruited, the more vulnerable individuals will tend to die first; if this effect predominated, it would result in a decrease in the average natural mortality rate with age. Thus, in a general theoretical treatment, allowance must be made for the possibility of M either increasing or decreasing with age.

In addition to a continuous trend of M, there is also the possibility of it changing suddenly at one or more stages during the life of the fish. For example, in a case where the drain of spawning caused an increase in the natural mortality rate with age, this trend would begin at the age of first maturity. Again, a discontinuity would arise if natural mortality were due to predation that was sharply restricted to fish of a certain size-range.

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*Huntsman (1948) mentions prolonged exposure to *high* temperature as a cause of death of salmon, but so far as we are aware there is no evidence that this, or some of the other causes he mentions, such as over-exertion and changes in salinity, occur in marine fish.

†The importance of epizootics in producing large fluctuations and cycles of abundance in wild animal populations has been documented by Elton (1931).

As might be expected from the scarcity of information on natural mortality in fish populations, it is not easy to find examples which demonstrate the form taken by a trend of *M* with age, but the few cases that have been investigated seem to give a fairly clear indication of what is to be expected. Ricker (1949a) has summarised age-composition data relating to several little-exploited species of fish in American lakes* and has drawn attention to the fact that the survival rates decreased with age in all cases. In three of these, viz.: the whitefish (*Coregonus clupeaformis*) of Lakes Opeongo and Shakespeare Island and the sauger (*Stizostedion canadense*) of Lake Nipigon, the data cover a sufficient range of age to enable the trend to be distinguished, and the survival rates converted to exponential mortality coefficients (i.e. estimates of *M*) are shown plotted against age in Fig. 7.1. Two examples from marine fish of mortality trends which are probably due mainly to natural causes are available in addition; the Pacific herring (*Clupea pallasii*) studied by A. L. Tester and cited by Ricker (1948), and the East Anglian herring (*Clupea harengus*) investigated by Hodgson (1932). The change of *M* with age in these species is also shown in Fig. 7.1. In two of these cases (the East Anglian herring and the whitefish of L. Opeongo) the trend can be accurately represented over the range of age concerned by a single linear regression. In the whitefish of Shakespeare Island Lake and the sauger of L. Nipigon, the estimates of *M* appear to comprise two separate linear trends, as indicated in the diagram. Only in one instance, the Pacific herring, does the trend appear to be markedly curvilinear, though even here a linear regression would give a reasonable approximation to the effects of the variation of *M* with age in a population model.

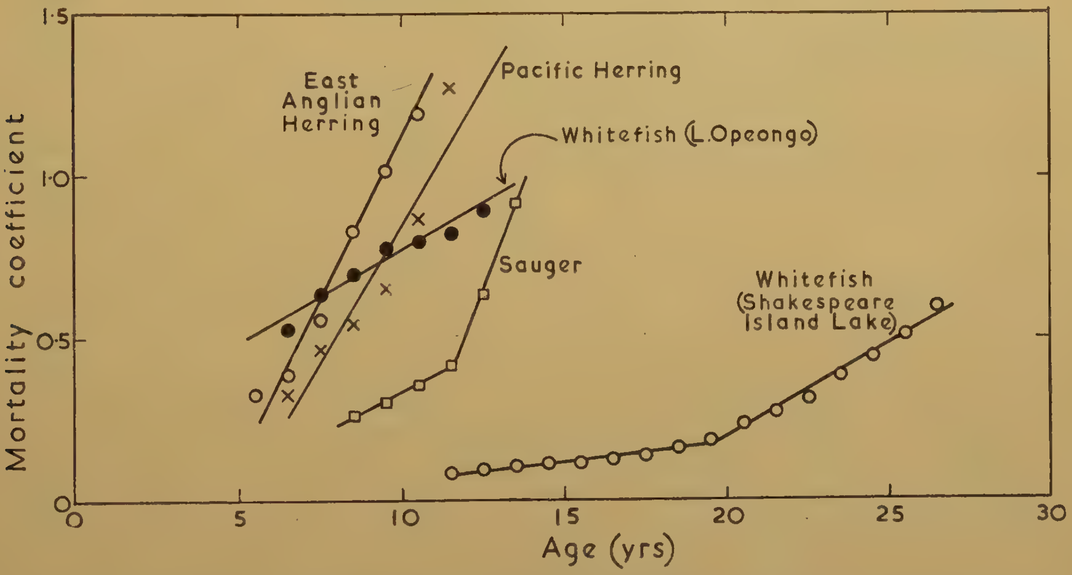

FIG. 7.1 TRENDS IN NATURAL MORTALITY WITH AGE

[These are examples taken from published data (see text for sources) of mortality in populations that were either not fished or in which fishing mortality was probably small compared with natural mortality. In only one case does the trend appear to be significantly curvilinear.]

It should be noted that a peculiarity common to all the above examples is that the age-composition data were obtained from samples caught by gill-net. Although Ricker is satisfied that in the examples cited by him the higher age-groups to which the mortality estimates refer were sampled fairly representatively, conclusions drawn from the data would be greatly strengthened if the same kind of trend were found in a species sampled by trawl gear. Nevertheless, it is difficult to see how sampling bias could be responsible for the trend over as wide a range of age as that in the Shakespeare Island whitefish, or for that matter how the marked trend in the East Anglian herring data could be caused by the relatively small contribution of fishing to the total mortality coefficient in that species.

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*Ricker uses data published by Hart, Hile and Kennedy, references to which will be found in his paper.

From the available evidence it would therefore seem that a satisfactory theoretical treatment of the variation of M with age in the exploited phase can be obtained by using one, or if necessary two, linear regressions. Thus for the cases in which the changes in M can be described by a single regression, the coefficient M of (3.1) can be expressed in the form

$$M_t = m_0 \pm m_1 t \quad \dots \quad (7.1)$$

valid between ages t_ρ and t_λ, in which the *value* of m_1 is always positive and is thus, strictly, not the slope of the regression but is the value of the slope of the regression, given a positive sign. This distinction is necessary owing to the fact that the integration required to obtain (7.5) below must be performed differently according to whether the sign of m_1 is positive or negative. The rate of decrease in number of the pre-exploited phase of the population becomes

$$\frac{dN}{dt} = -\left(m_0 \pm m_1 t\right)N \quad \dots \quad (7.2)$$

giving

$$R' = Re^{-(m_0\rho \pm \frac{1}{2} m_1 \rho^2)} \quad \dots \quad (7.3)$$

Similarly, for the exploited phase we have

$$\frac{dN}{dt} = -\left(F + m_0 \pm m_1 t\right)N$$

and the annual yield is given by the equation

$$Y_W = FR'\int_0^\lambda w_{t_{\rho'}+\psi} \cdot e^{-\left\{(F+m_0)\psi \pm \frac{1}{2} m_1 \psi^2\right\}}$$

$$= FR'W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_{\rho'}-t_0)} \int_0^\lambda e^{-\left\{(F+m_0+nK)\psi \pm \frac{1}{2} m_1 \psi^2\right\}} d\psi \quad \dots \quad (7.4)$$

Integration* gives

$$Y_W = FR'W_\infty \sqrt{\frac{2}{m_1}} \sum_{n=0}^{3} \Omega_n e^{-nK(t_{\rho'}-t_0)} \Big[I \Big]_{H_1}^{H_2} \quad \dots \quad (7.5)$$

The particular form of the term $\Big[I \Big]_{H_1}^{H_2}$ of (7.5) depends on the sign of m_1:—

(i) If $M = m_0 + m_1 t$ we have

$$R' = Re^{-(m_0\rho + \frac{1}{2} m_1 \rho^2)}$$

and

$$\Big[I \Big]_{H_1}^{H_2} = e^{+H_1^2} \int_{H_1}^{H_2} e^{-z^2} dz$$

---

*According to whether $M = m_0 \pm m_1 t$, we may make the substitution

$$\psi\sqrt{\frac{m_1}{2}} \pm \frac{F + m_0 + nK}{\sqrt{2m_1}} = Z$$

which allows the integrand to be reduced to the form

$$\int_{H_1}^{H_2} e^{\mp z^2} dZ$$

If $M = m_0 - m_1 t$ the value of m_1 and that of λ must be such that

$$m_1 t_\lambda \leqslant m_0$$

since if this were not so the mortality coefficient would be negative over part of the life-span.

where

$$H_1 = \frac{F + m_0 + nK}{\sqrt{2m_1}} \quad ; \quad H_2 = H_1 + \lambda\sqrt{\frac{m_1}{2}}$$

The integral $\int_0^H e^{-z^2}dz$ will be recognized as a form of the probability integral, and is tabulated as $erf\,(H)$, where $erf\,(H) = \frac{2}{\sqrt{\pi}}\int_0^H e^{-z^2}dz$ (see, e.g. Comrie (1949)).

(ii) If $M = m_0 - m_1 t$ we have

$$R' = Re^{-(m_0\rho - \frac{1}{2}m_1\rho^2)}$$

and

$$\left[I_{H_1}^{H_2}\right] = e^{-H_1^2}\int_{H_1}^{H_2} e^{+z^2} . dz$$

where

$$H_1 = -\frac{F + m_0 + nK}{\sqrt{2m_1}} \quad ; \quad H_2 = H_1 + \lambda\sqrt{\frac{m_1}{2}}$$

The integral $\int_0^H e^{+z^2}dz$ is met with less commonly than the probability integral, but has been tabulated up to $H = 4$ (e.g. Terrill and Sweeney, 1944) which will probably be sufficient for most purposes. An expansion of the function in a form suitable for computation is given by Dawson (1898) by means of which a value for $H > 4$ may be computed as required.

Where two regressions are needed to represent the change of M with age the problem is treated in a similar way except that the population is split into two sections corresponding to the age-range covered by each regression. If the discontinuity occurs at, say, age t_1, then for the younger section we have

$$M_t = m_0 + m_1 t$$

for values of t between t_ρ and t_1, and for the older section

$$M_t = m_0 + m_1 (t_1 - t_\rho) + m_2 t$$

for t between t_1 and t_λ. The values of either of the coefficients m_1 or m_2 may be negative.

Some indirect support for our treatment of natural mortality in fish is obtained from the fact that the above population model, in which the natural mortality coefficient is postulated as changing linearly with age, can produce age-structures which closely resemble the sigmoid survivorship (l_x) curves characteristic of populations of many animals, including man (Pearl, 1940). Furthermore, Leslie and Ranson (1940) have found that a mortality coefficient increasing proportionally with age gives a satisfactory representation of the survivorship curve of a population of voles (*Microtus agrestis*), and these authors mention that the same procedure gives a good fit in the case of *Drosophila* (data from Pearl and Parker, 1924).

7.2.2 *The maximum age, t_λ*

While dealing with the variation of the natural mortality coefficient with age we should discuss briefly certain points concerning the maximum age t_λ. In practice, it will often be possible to put $t_\lambda = \infty$ in equations in which this parameter appears (for example, when the total mortality rate is high) without producing any significant discrepancy, and thereby achieve considerable simplification. Further, the use of population models in which $t_\lambda = \infty$ may enable an assessment to be made of the maximum error which could have been introduced by giving t_λ a finite value (see §17.5.2). Although the procedure of making t_λ infinite may in many cases be justifiable biologically (see Bidder, 1925) since the occurrence of death from senescence has only been shown in very few species, Blackburn (1950) has investigated a species of whitebait (*Lovettia seali* Johnson) in which the duration of life is a single year only, and there is evidence that very few East Anglian herring survive to an age greater than about 12 years (Hodgson, 1947). For a further discussion of the subject of Old Age and Natural Death, the reader is referred to an article with this title by Medawar (1946).

It should be noted that, in theory, the populations represented by models in which t_λ is infinite can never reach a steady state and contain an infinite number of age groups, though these facts will not affect the usefulness of this simplification if employed with care. The source of greatest error, as we have already mentioned in §3.2, is its use in models containing factors expressed in a form that does not represent satisfactorily the characteristics of fish of high ages. This is the case with the exponential growth formula used by Ricker (1944), and other growth formulae such as the simple cubic used by Baranov (1918), in which the weight of an individual does not tend to a finite limit with increasing age; the implications of the procedure are demonstrated in §17.8. In general, postulating an infinite maximum age is likely to be most satisfactory when the natural mortality rate is treated as increasing linearly with age, but if (7.5) is used with M decreasing with age it is essential to use a value of t_λ such that M does not become negative.

7.3 DEPENDENCE OF THE NATURAL MORTALITY COEFFICIENT ON POPULATION DENSITY

In §6.1 we considered this problem in connection with pre-recruit mortality, but here we are concerned with its bearing on the reaction of the post-recruit phase to exploitation. We know of no definite evidence showing the dependence on density of the natural mortality rate in adult fish populations. There is, however, some indication that such a relationship may exist during the marine life of the Pink Salmon, *Oncorhynchus gorbuscha* (Pritchard, 1948), and Alm (1946) concludes that the natural mortality rate of perch in certain Swedish lakes may be a little greater where the population density is highest. Studies on the growth of experimental populations have shown this phenomenon to exist, and it is reasonable to suppose that it contributes to the maintenance of a steady state in a natural population as well as to the sigmoid growth of experimental populations. Moreover, several authors, e.g. Ricker (1940) and Kesteven (1947a) have stressed the need to take this aspect of natural mortality into account when setting up theoretical models of exploited fish populations.

Kostitzin (1939), summarising evidence from experimental studies, concludes that a linear relationship between the natural mortality rate and density is in best accordance with the data. In these circumstances we shall put

$$M = \mu_1 + \mu_2 N \qquad \text{.. .. .. ..} \qquad (7.6)$$

so that the rate of decrease in number due to natural mortality becomes

$$_M\left(\frac{dN}{dt}\right) = -\left(\mu_1 N + \mu_2 N^2\right) \qquad \text{.. .. ..} \qquad (7.7)$$

In so far as a high density may lead to harmful effects through 'overcrowding',* e.g. the more rapid spread of disease, we should expect the coefficient μ_2 to be positive, since the term N^2 of (7.7) can be taken as referring to the mutual 'interaction' of the individuals comprising the population, i.e. to the intra-specific density effect. On the other hand, if there is considerable predation—an interspecific component of the natural mortality—it does not necessarily follow that μ_2 will be positive. Thus when the density is low the food supply to the predator population will be smaller and its feeding intensity would be expected to increase; in other words, the predator might search more actively for its food (see §9.4.3.2). If this happened the natural mortality rate might decrease as the population density increased. The following methods are, however, applicable to either case.

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*It has been suggested that the density dependence of natural mortality may arise through competition for food, death presumably being due directly to starvation or perhaps to the susceptibility to disease resulting from under-nourishment. Examples of observations on adult animals that support this hypothesis are difficult to find. Even when starvation is apparently the cause of death the circumstances may be complex, as when Longhurst, Leopold and Dasmann (1952) found that deer which had thus died nevertheless had full stomachs, but as a result of overpopulation had been forced to eat a poor-quality food normally avoided.

A rigorous treatment of the general case, in which the population in the exploited area comprises both a pre-exploited and an exploited phase, is complex and leads to population models which are not convenient for general use. By making certain approximations a model of general applicability can be developed which, in most cases, provides an adequate representation of the problem (§7.3.1). If the numbers in the pre-exploited phase can be neglected by comparison with those in the exploited phase, a rigorous treatment is still complex, but it has been taken far enough in §7.3.2 to provide some check, in a given case, on the validity of the simple methods of §7.3.1.

7.3.1 *An approximate method using the annual mean number* $\bar{P}_N$

If we approximate to the number present at any time during a year by the annual mean number, $\bar{P}_N$, we can write (7.6) in the form

$$M = \mu_1 + \mu_2 \bar{P}_N \quad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (7.8)$$

with $\bar{P}_N$ given by (5.5), i.e.

$$\bar{P}_N = R\left\{\frac{1 - e^{-M\rho}}{M} + \frac{e^{-M\rho}(1 - e^{-(F+M)\lambda})}{F + M}\right\} \quad \ldots \quad \ldots \qquad (7.9)$$

If the values ${}_1M$ and ${}_2M$, corresponding to two levels of population abundance ${}_1\bar{P}_N$ and ${}_2\bar{P}_N$, are known, then we have the simultaneous equations

$${}_1M = \mu_1 + \mu_2({}_1\bar{P}_N)$$

and

$${}_2M = \mu_1 + \mu_2({}_2\bar{P}_N)$$

which provide solutions for μ_1 and μ_2. Alternatively, if a series of values of M and $\bar{P}_N$ are available, μ_1 and μ_2 can be obtained by fitting a linear regression, as discussed in §14.3.1. Equations (7.8) and (7.9) can then be used to obtain by iterative methods a unique solution for M corresponding to any given value of the fishing mortality coefficient, F, or mesh size, $t_{\rho'}$ (see §18.2). Since, in practice, direct estimates of the total number in a population will seldom be available, some modification of this procedure is required, though the principle remains the same. These details are discussed in connection with the use of data in §18.2, but we may note here that the annual mean number present per recruit, i.e. $\bar{P}_N/R$, is a more readily available statistic than the absolute number, $\bar{P}_N$, and we accordingly use a modified form of (7.8), viz.:

$$M = \mu_1 + \left(\mu_2 R\right)\frac{\bar{P}_N}{R}$$

the constants determined from data being μ_1, and $\mu_2 R$.

There is one special case in which a direct solution for M can be obtained, the conditions being that the number in the pre-exploited phase can be neglected, i.e. that $t_\rho = t_{\rho'}$, and that t_λ can be put to infinity. Then from (7.9)

$$\bar{P}_N = \frac{R}{F + M}$$

and hence, from (7.8), we have the quadratic

$$M^2 + M(F - \mu_1) - \mu_1 F - \mu_2 R = 0$$

Since the negative root of this equation has no meaning in the present context, a solution for M is given by the equation

$$M = \frac{1}{2}\left\{\mu_1 - F + \sqrt{(F - \mu_1)^2 + 4(\mu_1 F + \mu_2 R)}\right\} \quad \ldots \quad \ldots \quad (7.10)$$

7.3.2 *The equivalent constant natural mortality coefficient, $\underline{M}$*

The use of the annual mean numbers, $\bar{P}_N$, as an index of density is an example of a valuable technique used extensively in §9.4 when analysing the more complex relationship between growth and density. In this latter case we use the annual mean biomass $\bar{P}_W$ instead of $\bar{P}_N$, but the principle remains the same. While this is likely to give a close approximation to the true situation in most cases, it will not necessarily give unbiased assessments, and while on the question of the density dependence of the natural mortality coefficient it is worth while outlining a more exact treatment of the problem. The method we describe is concerned with obtaining an expression for an *equivalent constant coefficient*, $\underline{M}$, defined as that which would produce the same decrease in numbers during a year as that required by (7.7).

We consider an equilibrium population in which the abundance of the pre-exploited phase can be neglected in comparison with that of the exploited phase, and to which there is a constant annual recruitment R' on date $\tau_{\rho'}$. The rate of decrease in numbers of this population after any time ϕ has elapsed subsequent to date $\tau_{\rho'}$ is given by

$$\frac{dN}{d\phi} = -(F + \mu_1)N - \mu_2 N^2$$

and integration gives

$$N_\phi = \frac{1}{\dfrac{\mu_2}{F + \mu_1}\left(e^{(F + \mu_1)\phi} - 1\right) + \dfrac{e^{(F + \mu_1)\phi}}{N_0}}$$

where N_0 is the number present at the beginning of the year, i.e. on date $\tau_{\rho'}$. The number remaining at the end of the year is therefore

$$N_1 = \frac{1}{\dfrac{\mu_2}{F + \mu_1}\left(e^{(F + \mu_1)} - 1\right) + \dfrac{e^{(F + \mu_1)}}{N_0}} \quad \ldots \quad \ldots \quad (7.11)$$

We now require to express N_0 and N_1 in terms of the annual recruitment, R', the fishing mortality F, and the constant equivalent natural mortality coefficient, $\underline{M}$. If we can make the simplification of putting $t_\lambda = \infty$, then

$$N_0 = N_1 + R' \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (7.12)$$

and $\underline{M}$ is defined by the equation

$$N_1 = N_0 e^{-(F + \underline{M})} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (7.13)$$

From (7.11) and (7.12) we can eliminate N_1, and obtain a quadratic in N_0, of which the positive root is

$$N_0 = \frac{1}{2}\left\{R' - \frac{F + \mu_1}{\mu_2} + \sqrt{\left(\frac{F + \mu_1}{\mu_2} - R'\right)^2 + \frac{4R'(F + \mu_1)e^{(F + \mu_1)}}{\mu_2(e^{(F + \mu_1)} - 1)}}\right\}$$

and dividing by R' gives

$$\frac{N_0}{R'} = \frac{1}{2}\left\{1 - \frac{F + \mu_1}{\mu_2 R'} + \sqrt{\left(\frac{F + \mu_1}{\mu_2 R'} - 1\right)^2 + \frac{4(F + \mu_1)e^{(F + \mu_1)}}{\mu_2 R'(e^{(F + \mu_1)} - 1)}}\right\} \quad \ldots \quad (7.14)$$

which, for brevity, we write as Z. Further, we may eliminate N_1 from (7.12) and (7.13), giving

$$\frac{N_0}{R'} = \frac{1}{1 - e^{-(F+\underline{M})}} \quad \ldots \quad \ldots \quad \ldots \quad (7.15)$$

Finally, eliminating N_0/R' from (7.14) and (7.15) gives

$$\underline{M} = \log\left(\frac{Z}{Z-1}\right) - F \quad \ldots \quad \ldots \quad \ldots \quad (7.16)$$

Equation (7.16) provides a value of $\underline{M}$ for any given value of F, which can be used at once in (4.4) in place of the usual coefficient M to calculate the annual yield, there being no need for the iterative procedure required by the methods §7.3.1. To determine values of μ_1 and $\mu_2 R'$ in the first instance, it would be necessary to have estimates of the total mortality coefficient for at least two levels of population abundance together with the associated fishing mortality coefficients, as discussed previously.

SECTION 8: FISHING MORTALITY AND EFFORT

8.1 VARIATION OF THE FISHING MORTALITY COEFFICIENT, F, WITH AGE

It is convenient to distinguish three problems which involve the variation of the fishing mortality coefficient with age. The first (§8.1.1), concerns the effects of the selective action of the meshes of the fishing gear, and of the interaction between this and recruitment to the exploited area. The second (§8.1.2), is the change with age in the probability of capture following an encounter with gear, in so far as escape of fish by any means other than through the meshes is concerned. Finally (§8.1.3), there is the problem of heterogeneous fishing effort, i.e. a population exploited by more than one fleet, each of which is using a different size of mesh, thus introducing sudden changes in the fishing mortality when certain ages are reached.

8.1.1 *Mesh selection*

8.1.1.1 *Knife-edge selection*

We deal first with the general principles involved in incorporating into population models changes in gear selectivity, and retain, for the moment, the 'knife-edge' representation of the selection ogive, introduced in Part I.

A change in mesh size will, in general, have two effects. The first will be a change in the size of fish—and hence in the age—at which they first become retained by the net, and the second will be a change in the fishing mortality as a result of any difference in the fishing power of the gear with the changed mesh size. The equilibrium annual yield before a mesh change takes place is given, with the methods of §4, by the equation

$${}_1Y_W = F_1 W_\infty R e^{-M({}_1t_{\rho'} - t_\rho)} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_1t_{\rho'} - t_0)}}{F_1 + M + nK} \left(1 - e^{-(F_1 + M + nK)(t_\lambda - {}_1t_{\rho'})}\right)$$

and if the mesh change results in a new age at entry to the exploited phase, ${}_2t_{\rho'}$, and a new fishing mortality F_2, then the new equilibrium yield, ${}_2Y_W$, is given by the same expression altered accordingly. For the majority of species, it seems that the main selective action of a trawl takes place in the cod-end, and experimental work has been mainly concerned with an investigation of the effects of different sizes of cod-end mesh. The data for several species summarised by Jensen (1949) and also those given in §14.2.1 for plaice, show that there is, to a close approximation, a proportional relationship between the mean length, $L_{\rho'}$, at which fish are first retained, and the size of cod-end mesh. We can therefore write

$$L_{\rho'} = b \times (\text{mesh size}) \qquad .. \qquad .. \qquad .. \qquad (8.1)$$

where b is a constant which we call the *selection factor*. Now the age $t_{\rho'}$ corresponding to length $L_{\rho'}$, depends upon the growth rate of the species in question, and is given, from (3.8) by

$$t_{\rho'} = t_0 - \frac{1}{K} \log \left(1 - \frac{L_{\rho'}}{L_\infty}\right) \qquad .. \qquad .. \qquad .. \qquad (8.2)$$

Equations (8.1) and (8.2) give the value of $t_{\rho'}$ corresponding to any given cod-end mesh size, and contain parameters which can all be estimated from data.

The relationship between fishing power of trawls and size of mesh is more difficult to deal with, and we do not know of any experiments which have been carried out especially to establish it. Certain relevant information is available incidentally from experiments designed to test the selectivity of different sizes of cod-end mesh (see §14.2), which indicate that some change in fishing power probably does occur, though its occurrence is not consistent and the available data are insufficient to determine the form of the relationship. We can, however, draw one conclusion at this stage, namely that in so far as the fishing power of a trawl or similar gear is dependent on the resistance of the net to the flow of water, and hence to the rate of flow of water through it, it is likely that fishing power would increase asymptotically to a maximum value as the size of mesh increased.

8.1.1.2 *The linear approximation to an ogive*

We now consider in more detail the change in fishing mortality with age resulting from the selective action of trawls, which we have hitherto represented by assuming that the probability of capture, and hence the fishing mortality, is zero for fish of length less than the 50% point of the selection ogive, and constant for all sizes above this. An experimentally obtained selection ogive gives a measure of the probability of capture as a function of length; Buchanan-Wollaston (1927) has pointed out that its general shape is similar to that of an integrated normal curve, and suggested that this would be expected from the fact that there is a large element of chance in the process of escape.* We require the curve of selection as a function of age instead of length, and this may be obtained, if the growth rate of the species is known, by converting length to age by means of (8.2). Since growth over a short range of length in most species is approximately linear, the resulting age-ogive will not depart appreciably from the shape of the original length-ogive.

A closer approximation than the 'knife-edge' to the effect of an age selection ogive can be obtained by representing the probability of capture as increasing linearly with age over the selection range up to a certain point, after which it remains constant. It is convenient for this regression line of F on t to pass through the point of inflection of the ogive and to have the same slope, k_1 at that point, as shown in Fig. 8.1. If we define by t' the age at which this line cuts the t -axis, and by t'' the age at which the regression reaches the asymptotic value of the ogive, we have

$$F(t) = o; \text{ for } t < t'$$

$$F(t) = k_1 (t - t'); \text{ for } t' \leqslant t < t''$$

$$\text{and } F(t) = k_1 (t'' - t') = F_\infty; \text{ for } t'' \leqslant t < t_\lambda$$

The discontinuity in the variation of F with age which is thus supposed to occur at $t = t''$ makes it necessary to evaluate the yield over the age ranges t' to t'' and t'' to t_λ separately.

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*This matter is discussed further in §14.2.3.

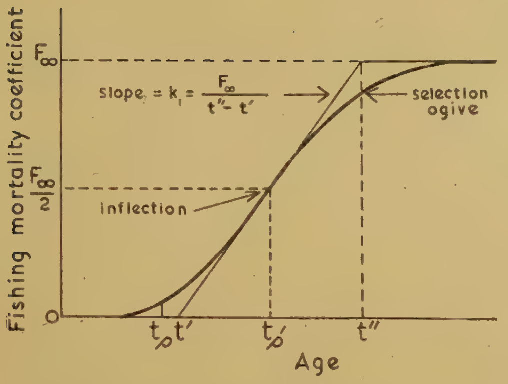

FIG. 8.1 THE LINEAR APPROXIMATION TO A SELECTION OGIVE

[In this method a linear regression of F on t is drawn so that it passes through the 50% point of the selection ogive and has there the same slope.]

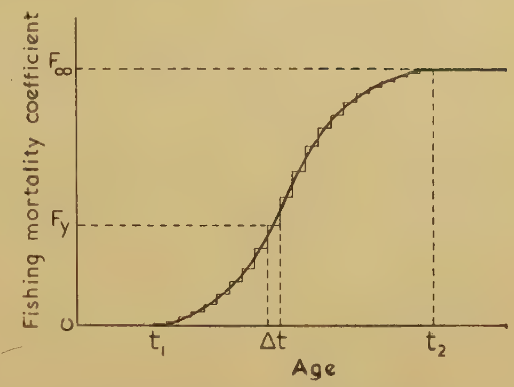

FIG. 8.2 THE DISCONTINUOUS APPROXIMATION TO A SELECTION OGIVE

[In this method F is made to increase with t in a series of short 'steps' over the selection range; the yield during each is calculated separately and these are summed to give the total yield. This approximation to a selection ogive can be as accurate as desired by making each 'step' sufficiently small, and can be applied to selection curves of any shape (see Figs. 8.3).]

Putting $t - t' = \psi$ and $t - t'' = \psi'$, the annual yield over the whole fishable life-span, from age t' to t_λ becomes

$$Y_W = k_1 N_{t'} \int_0^{t''-t'} w_{\varphi+t'} \cdot \psi e^{-(\frac{1}{2}k_1\varphi^2 + M\varphi)} d\psi + F_\infty N_{t''} \int_0^{t_\lambda - t''} w_{\psi'+t''} \cdot e^{-(F+M)\psi'} d\psi'$$

where $$N_{t'} = Re^{-M(t'-t_\rho)}$$

and $$N_{t''} = N_{t'} e^{-\frac{1}{2}k_1(t''-t')^2 - M(t''-t')}$$

Integration (cf. (7.3) with m_1 positive), gives

$$Y_w = RW_\infty e^{-M(t'-t_\rho)} \sum_{n=0}^{3} \Omega_n e^{-nK(t'-t_0)} \left[1 - \sqrt{\pi} H_1 e^{H_1{}^2} \Big(erf(H_2) - erf(H_1) \Big) \right.$$
$$\left. - e^{H_1{}^2 - H_2{}^2} \left\{ 1 - \frac{F_\infty(1 - e^{-(F_\infty + M + nK)(t_\lambda - t'')})}{F_\infty + M + nK} \right\} \right] \quad .. \quad (8.3)$$

where $$H_1 = \frac{M + nK}{\sqrt{2k_1}} \; ; H_2 = H_1 + (t'' - t')\sqrt{\frac{k_1}{2}}$$

It will be seen that if the selection ogive is regarded as the integrated form of a normal curve, the quantity $t'' - t'$ is proportional to the standard deviation σ. The conditions for 'knife-edge' selection are that $\sigma =$ zero, and therefore that

$$t'' - t' = \text{zero (i.e. } t' = t'' = t_{\rho'})$$

and hence $$k_1 = \infty$$

Making these substitutions in (8.3) reduces the latter to (4.4), as required.

8.1.1.3 *The discontinuous approximation to an ogive*

The conditions in which the 'knife-edge' or linear regression approximations to a selection ogive are least satisfactory are where the selection range occupies an appreciable proportion of the fishable life-span, or where there is a high total mortality rate, since in both cases most of the yield would consist of fish within the selection range of size. The most exact method of representing the variation of F with age over the selection range is to treat it as discontinuous, the ogive being divided into a large number of short periods during each of which F is taken as constant, as shown in Fig. 8.2. This method has the advantage that the selection ogive need not conform to the shape of an integrated normal curve; it is therefore applicable to the modified selection curves resulting from the interaction of migration to the exploited area and selection by the gear, discussed in §8.1.1.4, which may differ markedly from a normal ogive.

We denote by t_1 the age below which the fishing mortality can be considered to be negligibly small, and by t_2 the age at which it reaches its asymptotic value. The effective duration of selection, λ', is

$$\lambda' = t_2 - t_1$$

We suppose that this period is divided into $\lambda'/\Delta t$ equal parts, and that if R individuals are present at age t_ρ, where $t_\rho < t_1$, the number present at age t_1 can be defined as

$$N_1 = Re^{-M(t_1 - t_\rho)}$$

The number present at age $t_1 + \Delta t$ will be

$$N_2 \simeq N_1 e^{-(F_1 + M)\Delta t}$$

where F_1 is the fishing mortality at age $t_1 + \Delta t/2$, and, in general, the number present at age $t_1 + y\Delta t$ will be

$$N_{y+1} \simeq N_y \,.\, e^{-(F_y + M)\Delta}$$

where F_y is the fishing mortality at age $t_1 + (y - 1/2)\Delta t$. The yield over the yth increment can therefore be written as

$$(Y_W)_y \simeq F_y \,.\, w_y \,.\, N_y \int_0^{\Delta t} e^{-(F_y + M)t} dt \qquad \ldots \quad \ldots \quad (8.4)$$

where w_y is defined in the same way as F_y, and is the weight of an individual at age $t_1 + (y - 1/2)\Delta t$.

The annual yield from fish within the selection range is therefore given by

$$ {}_AY_W \simeq \sum_{y=1}^{\lambda'/\Delta t} (Y_W)_y = \sum_{y=1}^{\lambda'/\Delta t} \frac{F_y \,.\, w_y \,.\, N_y}{F_y + M}\left(1 - e^{-(F_y + M)\Delta t}\right) \qquad \ldots \quad (8.5)$$

where

$$N_y = Re^{-M\{t_1 + (y-1)\Delta t - t_\rho\} - \sum_{x=1}^{y-1} F_x \Delta t} \qquad \ldots \quad \ldots \quad (8.6)^*$$

If the growth of fish within the selection range can be adequately represented by (3.7), then we can write

$$(Y_W)_y \simeq F_y N_y W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK\{t_1 + (y-1)\Delta t - t_0\}} \int_0^{\Delta t} e^{-(F_y + M + nK)t} dt$$

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*When $y = 1$ the limits of the summation term in the exponent are 1 to 0. In this case there are no terms in the summation, and its value will be taken as zero. The same rule applies in some other equations of §8 having a summation term in the exponent, viz. (8.8), (8.11), (8.12), (8.18), (8.19), (8.20) and (8.21).

in place of (8.4); the annual yield from fish within the selection range then becomes

$$_{A}Y_{W} \simeq W_{\infty} \sum_{y=1}^{\lambda'/\Delta t} F_{y} N_{y} \sum_{n=0}^{3} \frac{\Omega_{n} e^{-nK\{t_1 + (y-1)\Delta t - t_0\}}}{F_{y} + M + nK} \left(1 - e^{-(F_y + M + nK)\Delta t}\right) \quad .. \quad (8.7)$$

The yield from the rest of the population, i.e. between ages t_2 and t_λ is given by the usual equation, viz.

$$_{B}Y_{W} = F_{\infty} W_{\infty} N_{t_2} \sum_{n=0}^{3} \frac{\Omega_{n} e^{-nK(t_2 - t_0)}}{F_{\infty} + M + nK} \left(1 - e^{-(F_\infty + M + nK)(t_\lambda - t_2)}\right) \quad .. \quad (8.8)$$

where

$$N_{t_2} = Re^{-M(t_2 - t_\rho) - \sum_{x=1}^{\lambda'/\Delta t} F_x \Delta t}$$

and the annual yield from the whole population is

$$Y_{W} = {}_{A}Y_{W} + {}_{B}Y_{W}$$

8.1.1.4 *Resultant effect of recruitment and gear selection*

We have so far been dealing with the case in which fish enter the exploited area when their size is below the selection range of the gear in use, so that entry to the exploited phase of the population is decided only by the selective properties of the gear. The other extreme is that the recruitment migration takes place when fish have reached a size which is above the selection range, in which case entry to the exploited phase is determined only by the recruitment pattern. There remains for consideration the possibility that fish may migrate to the exploited area at a size, or over a range of size, that lies wholly or partly within the selective range of the gear. In the simplest case we may suppose that an entire year-class is recruited at the same size and age, resulting in exposure of fish to a certain proportion of the full fishing mortality as soon as they enter the exploited area. An hypothetical example of this is shown in Fig. 8.3.1, the full line giving the *resultant selection curve.* Since this resultant curve gives the proportion of the full fishing mortality to which a fish of a given age is exposed, it represents the true selection to the exploited phase, and the only modifications of the above methods required for its analysis are due to the difference in shape from the usual ogive. For example, if we wish to use the 'knife-edge' approximation it is no longer satisfactory to determine a 50% point, since this would not take account of the irregular shape of the resultant ogive; moreover, the 50% point no longer has the same significance if it should be that fish enter the exploited area at an age which is above the 50% selection age for the gear.

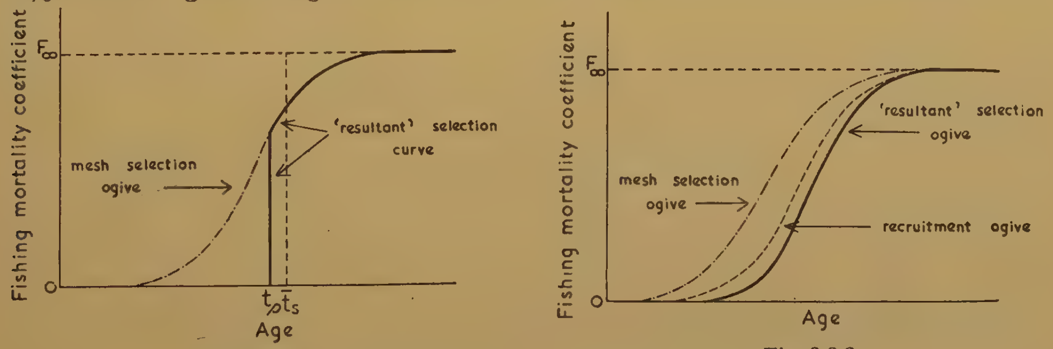

Fig. 8.3.1

Fig. 8.3.2

FIGS. 8.3 'RESULTANT' SELECTION CURVES

[If fish are recruited at a length, or over a range of length, that overlaps the selection range of the gear, the curve defining the relation between fishing mortality and age is called the 'resultant' selection curve. The shape of such a curve may be very different from the approximately symmetrical sigmoid curve obtained when only gear selection is operative.]

Fig. 8.3.1 'Knife-edge' recruitment at a length within the selection range of the gear.

Fig. 8.3.2 'Ogive' recruitment covering a range of length overlapping the selection range of the gear.

The most exact procedure in such a case would be to use the discontinuous approximation described in §8.1.1.3 which is applicable to a selection curve of any shape, but for most purposes it is sufficient and more convenient to adopt a modified 'knife-edge' approximation and to estimate the *mean* selection age, $\bar{t}_s$, instead of the median. This can be done by dividing the age axis within the selection range into a sufficient number of equal age intervals of magnitude and reading off the corresponding increments ΔF_1, $\Delta F_2 \ldots\ldots \Delta F_y \ldots\ldots \Delta F_z$ on the Y -axis. Denoting by t_y the age at the middle of the yth interval during which the increment on the Y -axis is ΔF_y, the mean selection age $\bar{t}_s$ is given by the expression

$$\bar{t}_s = \frac{\sum_{y=1}^{z} t_y \,.\, \Delta F_y}{\sum_{y=1}^{z} \Delta F_y} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (8.9)$$

It will be seen that for a symmetrical ogive, $\bar{t}_s$ is the same as the 50% selection age, which we have hitherto denoted by $t_{\rho'}$. Thus $\bar{t}_s$ has the same significance as $t_{\rho'}$ and may be used in place of the latter parameter in equations for yield. The position of $\bar{t}_s$ in Fig. 8.3.1 is indicated by the vertical broken line.

If recruitment of a year-class takes place over a range of age it is possible to construct an age recruitment ogive defining the probability that a fish of a given age will have entered the exploited area. Let us suppose that for a fish of age t this probability is p_t,* and that a fish of this age in the exploited area is exposed to a fraction y_t of the full fishing mortality F_∞. The effective fishing mortality coefficient to which all fish of age t are exposed, is given by the product $p_t.y_t.F_\infty$. A resultant selection ogive can therefore be constructed by multiplying the ordinates of the age recruitment ogive and the mesh selection ogive at each age, an hypothetical example being given in Fig. 8.3.2. It will be seen that this is the general form of which the previous example of 'knife-edge' recruitment is a special case; in the latter the value of p_t is zero until the recruitment age is reached, after which it is unity. Although resultant selection ogives of the kind shown in Fig. 8.3.2 are more regular in shape than when recruitment is 'knife-edge', they may nevertheless be markedly asymmetrical, and it is better to use the mean selection age than to take the 50% point. The North Sea plaice provides examples of resultant selection ogives (see §15.1.4).

8.1.2 *Avoidance of capture by means other than escape through the mesh*

During the course of recent mesh experiments on plaice, described in §14.2.1 evidence was obtained which suggested that, in addition to the purely selective action of the mesh, the probability of capture decreased as the size of fish increased. A phenomenon of this kind is to be expected with any method of capture which allows the behaviour of the fish themselves to influence their probability of capture following an encounter with the gear. A greater activity or swimming power of larger fish might be the cause, or possibly a conditioned behaviour as a result of previous encounters with gear; or, again, the progressive elimination of the more vulnerable fish from a brood which, on entry to the exploited phase, contained fish of differing intrinsic liabilities to capture. The effect of any of these factors is to introduce a decrease of the fishing mortality coefficient with age.†

It so happens that only a few simple functions $F_{(t)}$ can be introduced into the theoretical models we have developed without resulting in undue mathematical complexity, and we here give an elementary treatment of the problem by using a single linear regression of F on t throughout the fishable life-span to represent the process of 'avoidance'. This is likely to meet the requirements of most cases, but a markedly non-linear variation could be suitably subdivided into shorter periods within each of which a linear regression would be satisfactory. It is unlikely that the fishable life-span would need to be divided into more than two, or at the most three, such periods. The theoretical methods required for an analysis of this problem are very similar to those used in §8.1.1.2 to represent a selection ogive by a linear regression, and in the following treatment both problems are considered simultaneously.

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*An alternative definition of p_t is the proportion of the total year-class that has entered the exploited area when age t is reached.

†According to Lack (1951) the mean annual mortality in adult birds is usually constant at all ages, but that of juveniles is higher, " . . . presumably due to their inexperience".

Since we should expect any avoidance factor to apply to fish within the selection range as well as above it, we may apply the linear regression of F on t representing avoidance from age t_1 (defined in §8.1.1.2) to age t_λ, as shown in Fig. 8.4. The ascending regression line is drawn, as before, through the point of inflection of the selection ogive, with the same slope as the latter at that point, so that it will still cross the t-axis at t'. The slope, however, is now $k_1 - k_2$, where k_2 is the coefficient of avoidance. Unless the value of k_2 is particularly large, it is convenient to terminate the ascending regression line when it has reached a value F', corresponding to the point t'' of Fig. 8.1, so that F' is given by

$$F' = F_\infty - k_2(t'' - t')$$

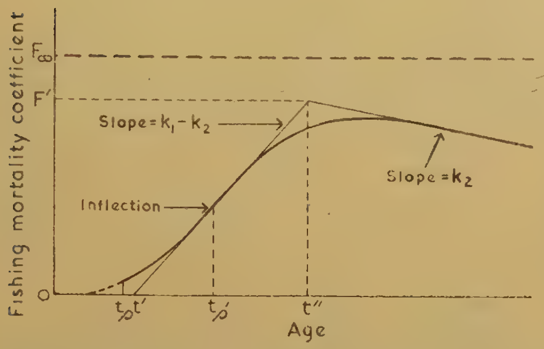

FIG. 8.4 THE LINEAR APPROXIMATION TO SELECTION AND AVOIDANCE

[Here it is supposed that fish are able to avoid capture to some extent by swimming out of the path of a trawl, this ability increasing with size of fish. This avoidance is superimposed on selection, the combined effect being represented by two linear regressions of F on t.]

We have, therefore, the following relationships:—

$$F(t) = o, \text{ for } t < t'$$

$$F(t) = (k_1 - k_2)(t - t'); \text{ for } t' \leqslant t < t''$$

$$F(t) = F' - k_2(t - t''); \text{ for } t'' \leqslant t < t_\lambda$$

With the same procedure as in §8.1.1.2, the equation for yield becomes

$$Y_W = (k_1 - k_2)N_{t'}\int_0^{t''-t'} w_{\psi+t'} \cdot \psi e^{-\{M\psi + \frac{1}{2}(k_1 - k_2)\psi^2\}}d\psi +$$

$$+ N_{t''}\int_0^{t_\lambda - t''} w_{\psi'+t''} \cdot (F' - k_2\psi')e^{-\{(F'+M)\psi' - \frac{1}{2}k_2\psi'^2\}}d\psi'$$

which, on integration [cf. (7.3) and (8.3)], gives

$$Y_W = RW_\infty e^{-M(t_1 - t_\rho)}\sum_{n=0}^{3}\Omega_n e^{-nK(t'-t_0)}\Bigg[1 - \sqrt{\pi}H_3 e^{H_3^2}\Big(erf(H_4) - erf(H_3)\Big)$$

$$- e^{H_3^2 - H_4^2}\left\{e^{H_6^2 - H_5^2} + \sqrt{\frac{2}{k_2}}\Big(M + nK\Big)e^{-H_5^2}\int_{H_5}^{H_6} e^{+z^2}dZ\right\}\Bigg] \quad .. \quad (8.10)$$

where

$$H_3 = \frac{M + nK}{\sqrt{2(k_1 - k_2)}}$$

$$H_4 = H_3 + (t'' - t')\sqrt{\frac{k_1 - k_2}{2}}$$

$$H_5 = -\frac{F' + M + nK}{\sqrt{2k_2}}$$

$$H_6 = (t_\lambda - t'')\sqrt{\frac{k_2}{2}} + H_5$$

8.1.3 *Heterogeneous fishing: the effects of the simultaneous use of gears with different selective properties*

To obtain an expression for the total yield from a population which is being fished by a number of fleets each using a different mesh size, we may proceed by methods similar to those used in §8.1.1.3. Suppose the different meshes used by the fleets correspond to the mean selection ages ${}_1t_{\rho'}$, ${}_2t_{\rho'}$, ${}_3t_{\rho'}$ etc.... ${}_rt_{\rho'}$, these values being in ascending order of magnitude. The fishing mortality effective between ages ${}_1t_{\rho'}$ and ${}_2t_{\rho'}$ will be due only to those fleets using mesh size ${}_1t_{\rho'}$, and we may designate this coefficient by F_1. The coefficient F_2, effective between ages ${}_2t_{\rho'}$ and ${}_3t_{\rho'}$, will be the sum of F_1 and the mortality due to fleets using mesh size ${}_2t_{\rho'}$, and so on. The yield from the population between ages ${}_1t_{\rho'}$ and ${}_rt_{\rho'}$ is therefore given by

$${}_AY_W = W_\infty \sum_{y=1}^{r-1} F_y N_y \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_yt_{\rho'} - t_0)}}{F_y + M + nK}\left(1 - e^{-(F_y + M + nK)({}_{y+1}t_{\rho'} - {}_yt_{\rho'})}\right) \quad .. \quad (8.11)$$

where

$$N_y = Re^{-M({}_yt_{\rho'} - t_\rho) - \sum_{x=1}^{y-1} F_x({}_{x+1}t_{\rho'} - {}_xt_{\rho'})}$$

The yield between ages ${}_rt_{\rho'}$ and t_λ is given by

$${}_BY_W = FW_\infty N_r \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_rt_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F + M + nK)(t_\lambda - {}_rt_{\rho'})}\right) \quad .. \quad (8.12)$$

where F is the fishing mortality coefficient generated by the combined fleets, and

$$N_r = Re^{-M({}_rt_{\rho'} - t_\rho) - \sum_{x=1}^{r-1} F_x({}_{x+1}t_{\rho'} - {}_xt_{\rho'})}$$

The total yield is therefore

$$Y_W = {}_AY_W + {}_BY_W$$

In addition to the total yield from the population, it may be necessary to evaluate the yield from one particular fleet. If this fleet is using a mesh corresponding to a value ${}_qt_{\rho'}$, where ${}_qt_{\rho'} \leqslant {}_rt_{\rho'}$, and if it generates a fishing mortality ${}_qF$, then the yield obtained by this fleet from fish between ages ${}_qt_{\rho'}$ and ${}_rt_{\rho'}$ is

$$\left({}_AY_W\right)_q = {}_qFW_\infty \sum_{y=q}^{r-1} N_y \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_yt_{\rho'} - t_0)}}{F_y + M + nK}\left(1 - e^{-(F_y + M + nK)({}_{y+1}t_{\rho'} - {}_yt_{\rho'})}\right) \quad .. \quad (8.13)$$

and from fish between ages ${}_rt_{\rho'}$ and t_λ

$$\left({}_BY_W\right)_q = {}_qFW_\infty N_r \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_rt_{\rho'} - t_0)}}{F + M + nK}\left(1 - e^{-(F + M + nK)(t_\lambda - {}_rt_{\rho'})}\right) \quad .. \quad (8.14)$$

where N_y and N_r are defined as before. Thus, the total yield obtained by the fleet in question is

$$_{q}Y_W = {}_{qA}Y_W + {}_{qB}Y_W$$

It will be seen from the above that the essential characteristic of heterogeneous fishing effort is that more than one size of mesh is in use simultaneously. If we have a population exploited by more than one fleet, but all vessels are using the same mesh size, the total yield is given by (4.4) with F referring to the total fishing mortality. The yield obtained by any one of these fleets is given by

$$\left(Y_W\right)_q = {}_qFRW_\infty e^{-M\rho}\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\left(1-e^{-(F+M+nK)\lambda}\right)$$

where $_qF$ is the fishing mortality coefficient generated by the fleet in question. Hence

$$\frac{(Y_W)_q}{Y_W} = \frac{_qF}{F} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (8.15)$$

where Y_W is the total yield from the population. The ratio of the yield obtained from a population by one of any number of fleets to the total yield is therefore the same as the ratio of the fishing mortality generated by that fleet to the total fishing mortality, provided all vessels are using the same size of mesh.

8.2 YEAR-TO-YEAR VARIATIONS IN THE FISHING ACTIVITY—TRANSITIONAL PHASES

In this section we discuss problems raised by annual variations in the magnitude of the fishing mortality and in its distribution with respect to age. The former can arise from a number of causes. Apart from the relatively rapid increase in effort that occurs when a fishery is developing, there are also progressive changes in efficiency of vessels or gear and in the size of fleets for economic reasons, that cause trends in the magnitude of the fishing mortality, even in a relatively well-established fishery. During the 1914-18 and 1939-45 wars, on the other hand, there was partial or complete cessation of fishing for a period of several years in fisheries which were, effectively, in a steady state prior to the outbreak of hostilities, thus involving rapid and extensive changes in the magnitude of the fishing mortality. In view of the importance of such oscillations and trends in presenting opportunities for a study of the influence of changes in population density on the dynamics of fish populations, it is necessary to have a method of analysing them.

Another important case of trend concerns the events immediately following the introduction of regulative measures. Regulation of fishing intensity involves changes in the magnitude of the fishing mortality, and mesh regulation results in changes in the distribution of the fishing mortality with respect to age and possibly in its magnitude also. Since the yield—and the values of other characteristics of the catch and population—immediately following either kind of regulation may be of quite a different magnitude to those relating to the new equilibrium, it is obviously desirable to be able to predict the changes during the transitional period.

The methods required for analysis of the effects of variations in fishing mortality, as in the case of recruitment and natural mortality, are extensions of those given in §4.2, since the yield from one year-class fished throughout its fishable life-span is not now the same as the annual yield from the whole population. Before undertaking a detailed treatment, we may point out two useful simplifications that are made. The first is the assumption that all changes in fishing mortality commence on the date on which fish enter the exploited phase. As in §4.2, therefore, the year over which the annual yield is measured commences on this date. The second concerns the representation of a fishing mortality that is changing continuously over a period of years. Since we are concerned here with deriving expressions giving the annual values of the yield, etc., we can obtain an adequate approximation by referring to the annual mean fishing mortality over each year and assuming that it changes abruptly from one year to the next. In §8.2.1 we deal with changes in fishing intensity only, and in §8.2.2 with changes in gear selectivity combined, in the general case, with an associated change in fishing power of the gear.

8.2.1 *Changes in fishing intensity*

The simplest of the situations resulting from a change in the magnitude of the fishing intensity is that in which the fishing mortality coefficient, F_0, after remaining constant for a period of sufficient length for a steady state to be attained, changes abruptly to a new value, F_1. Each age-group which existed just prior to the change will have been under the influence of the old fishing intensity for at least one year, but in each subsequent year the oldest year-class present will be lost from the population, so that, at the end of $\lambda - 1$ years, none of the original population remains. During this transitional period a new population will have been built up, all year-broods of which will have been under the influence of the new fishing intensity only; from the beginning of the λth year onward, these comprise the new equilibrium population.

With the terminology of §4.2 we can denote the number present in the exploited phase of the population after any time ϕ during the *first* year subsequent to the change in the fishing mortality from F_0 to F_1, by

$$R'e^{-(F_1+M)\phi}\left[\sum_{p=1}^{\lambda-1} e^{-(F_0+M)p} + 1\right]$$

and during the *second* year by

$$R'e^{-(F_1+M)\phi}\left[\sum_{p=2}^{\lambda-1} e^{-(F_0+M)(p-1)-(F_1+M)} + \sum_{q=0}^{1} e^{-(F_1+M)q}\right]$$

and, in general, the number present during the Xth year following the change, where $X \leqslant \lambda - 1$, is

$$R'e^{-(F_1+M)\phi}\left[e^{(F_0-F_1)(X-1)}\sum_{p=X}^{\lambda-1} e^{-(F_0+M)p} + \sum_{q=0}^{X-1} e^{-(F_1+M)q}\right]$$

The annual yield in number during the Xth year is therefore given by

$${}_XY_N = F_1R'\left[e^{(F_0-F_1)(X-1)}\sum_{p=X}^{\lambda-1} e^{-(F_0+M)p} + \sum_{q=0}^{X-1} e^{-(F_1+M)q}\right]\int_0^1 e^{-(F_1+M)\phi}d\phi$$

and performing the summations and integration gives

$${}_XY_N = \frac{F_1R'}{F_1+M}\left\{1 - e^{-(F_1+M)X} + e^{(F_0-F_1)(X-1)}\left(\frac{1-e^{-(F_1+M)}}{1-e^{-(F_0+M)}}\right)\times\left(e^{-(F_0+M)X} - e^{-(F_0+M)\lambda}\right)\right\} \quad \ldots \quad \ldots \quad \ldots \quad (8.16)$$

Similarly, the yield in weight during the Xth year is

$${}_XY_W = F_1R'W_\infty\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F_1+M+nK}\left\{1 - e^{-(F_1+M+nK)X} + e^{(F_0-F_1)(X-1)}\left(\frac{1-e^{-(F_1+M+nK)}}{1-e^{-(F_0+M+nK)}}\right)\left(e^{-(F_0+M+nK)X} - e^{-(F_0+M+nK)\lambda}\right)\right\} \quad (8.17)$$

In these and subsequent equations of §8.2.1, R' is given in the usual way by the equation

$$R' = Re^{-M\rho}$$

It will be seen that putting $F_0 = F_1$ reduces (8.16) and (8.17) to (5.5) and (4.4) respectively, as required.

We may now proceed to the more general case in which a series of yearly changes in fishing intensity occur. We shall assume, as before, that a complete population has been built up during a period of constant fishing, represented by the coefficient F_0, and that on date $\tau_{\rho'}$ the coefficient changes to F_1. In this case, however, further changes, to F_2, F_3, F_4 .... etc. take place on this date of each subsequent year. During the first $\lambda - 1$ years following the first change, $F_0 \to F_1$, the original population is still represented, though by a progressively decreasing number of age-groups. The number present during the year following the Xth of a series of yearly changes in intensity, i.e. when the fishing mortality coefficient is $F_X (X \leqslant \lambda - 1)$, is given by the above methods as

$$R'e^{-(F_X + M)\phi} \left[e^{F_0 X - \sum\limits_{u=0}^{X-1} F_u} \sum_{p=X}^{\lambda-1} e^{-(F_0+M)p} + \sum_{q=0}^{X-1} e^{-qM - \sum\limits_{u=X-q}^{X-1} F_u} \right] \quad .. \quad (8.18)$$

so that the annual yield during this year is

$$_XY_W = F_X R'W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}(1 - e^{-(F_X + M + nK)})}{F_X + M + nK} \left\{ \left(\frac{1 - e^{-(F_0 + M + nK)(\lambda - X)}}{1 - e^{-(F_0 + M + nK)}} \right) \times \right.$$

$$\left. \times e^{-(M+nK)X - \sum\limits_{u=0}^{X-1} F_u} + \sum_{q=0}^{X-1} e^{-(M+nK)q - \sum\limits_{u=X-q}^{X-1} F_u} \right\} \quad .. \quad (8.19)$$

When $\lambda - 1$ years have elapsed, the original population will have completely disappeared, and each year-class comprising the new population will have been depleted by a different fishing intensity during each year of its life in the exploited phase. The number present during the Xth year subsequent to the original change $F_0 \to F_1$, where $X > \lambda - 1$, is given, from the second term of (8.18), by

$$R'e^{-(F_X + M)\phi} \sum_{q=0}^{\lambda-1} e^{-qM - \sum\limits_{u=X-q}^{X-1} F_u} \quad .. \quad .. \quad (8.20)$$

and the annual yield by

$$_XY_W = F_X R'W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}(1 - e^{-(F_X + M + nK)})}{F_X + M + nK} \sum_{q=0}^{\lambda-1} e^{-(M+nK)q - \sum\limits_{u=X-q}^{X-1} F_u} \quad .. \quad (8.21)$$

these being the most general of the population models which take account of variations in fishing intensity.

Finally, let us suppose that the fishing mortality becomes stabilised at a value F_0' after a period during which time the fishing mortality has been changing each year. If the stabilisation occurs on date $\tau_{\rho'}$ of a certain year X' (i.e. $F_0' = F_{X'}$), there will follow a further period of $\lambda - 2$ years during which the original population is being superseded by a new one built up under the influence of the constant fishing mortality F_0'. During the Xth year following the original change $F_0 \to F_1$, where $X' \leqslant X \leqslant X' + \lambda - 2$, the number present will be

$$R'e^{-(F_0 + M)\phi} \left[\sum_{p=0}^{X-X'} e^{-(F_0' + M)p} + e^{-(F_0' + M)(X - X')} \sum_{q=1}^{\lambda - 1 - X + X'} e^{-qM - \sum\limits_{u=X'-q}^{X'-1} F_u} \right]$$

and the annual yield

$$
{}_XY_W = F_0{}'R'W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F_0{}'+M+nK} \Bigg\{ 1 - e^{-(F_0{}'+M+nK)(X-X'+1)} +
$$

$$
+ \left(1-e^{-(F_0+M+nK)}\right) e^{-(F_0{}'+M+nK)(X-X')} \sum_{q=1}^{\lambda-1-X+X'} e^{-(M+nK)q-\sum\limits_{u=X'-q}^{X'-1} F_u} \Bigg\} \quad \ldots \quad (8.22)
$$

Although we have been concerned primarily with expressions giving the annual yield in weight when there are oscillations or trends in the fishing intensity, equations giving other characteristics of the catch and population can be derived by similar methods, as exemplified by (8.16) for *the yield in number*. It may be noted that the *mean population number* and the *mean biomass* during any year X are given by the equations

$$
{}_X\bar{P}_N = \frac{R}{M}\left(1-e^{-M\rho}\right) + \frac{{}_XY_N}{F_X} \quad \ldots \quad \ldots \quad (8.23)
$$

and

$$
{}_X\bar{P}_W = RW_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_\rho-t_0)}}{M+nK}\left(1-e^{-(M+nK)\rho}\right) + \frac{{}_XY_W}{F_X} \quad \ldots \quad (8.24)
$$

Also, the catch per unit effort in year X is proportional to the mean biomass of the exploited phase during that year, ${}_XY_\mathbf{W}/F_X$, and the *mean weight of fish in the catch* in year X is

$$
{}_X\bar{W}_Y = \frac{{}_XY_W}{{}_XY_N} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (8.25)
$$

8.2.2 *Changes in selective properties of the gear*

The transitional phase following a change in gear selectivity can be analysed by methods similar to those used above for dealing with a change in the magnitude of the fishing intensity. Thus it is possible to obtain a generalized expression, comparable to (8.21), which will give the yield in any year during a period in which a series of yearly changes in mesh size are occurring, but this is complex and not suitable for computation. For this reason the following analysis is restricted to the case of a single change in gear selectivity, and more complex situations are best evaluated *ab initio* by similar methods.

As was pointed out in §8.1.1.1, an increase in mesh size will, in general, involve also an increase in the fishing power of the gear, and hence in the fishing mortality. We therefore suppose that a complete population has been built up under the influence of a fishing mortality F_0 and a mesh size corresponding to a value ${}_0t_{\rho'}$, and that on date ${}_0\tau_{\rho'}$ the mesh size is increased by all vessels to a value ${}_1t_{\rho'}$, the fishing mortality changing simultaneously to a value F_1. Fish will now enter the exploited phase of the population on date ${}_1\tau_{\rho'}$, and if we put

$$
{}_1t_{\rho'} - {}_0t_{\rho'} = V + v
$$

where V denotes a whole number of years, and v a fraction of a year, we have also

$$
{}_1\tau_{\rho'} - {}_0\tau_{\rho'} = v
$$

We define the annual yield as the yield over the year following the original date ${}_0\tau_{\rho'}$, and use the symbol ϕ to denote, as before, any fraction of a year which has elapsed following this date. After the mesh change, unless v = zero, the age-group that enters the exploited phase of the population will do so on date ${}_1\tau_{\rho'}$, and will therefore be fished only for a fraction, $1-v$, of the year. As in §8.2.1 we first derive expressions for the number present, and then give the annual yield in weight, putting for the latter equations, to avoid undue complexity;

$$F_0 + M + nK = \alpha$$

$$F_1 + M + nK = \beta$$

$$F_0 + F_1 + M + nK = \gamma$$

$$\text{and } M + nK = \delta$$

Immediately after an increase in mesh size has occurred the pre-exploited phase of the population will not only be longer than before, but will contain one or more year-classes whose numbers have been depleted by the original fishing mortality, F_0. We denote by R' the numbers of each year-class surviving to age ${}_0t_{\rho'}$, i.e.

$$R' = Re^{-M({}_0t_{\rho'} - t_\rho)}$$

and in the expressions for numbers present, it is necessary to consider fish between ages ${}_0t_{\rho'}$ and ${}_1t_{\rho'}$, as well as between ${}_1t_{\rho'}$ and t_λ. The life-span taken as reference will always be that obtaining before the mesh change occurs, so that denoting this by λ_0 we have

$$\lambda_0 = t_\lambda - {}_0t_{\rho'}$$

All the equations for yield derived below can be written in the form

$$Y_W = A\sum_{n=0}^{3} B_n C_n$$

where

$$A\sum_{n=0}^{3} B_n = F_1 W_\infty R e^{-M({}_0t_{\rho'} - t_\rho)} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_0t_{\rho'} - t_0)}}{F_1 + M + nK}$$

and we are concerned with evaluating C_n.

The number present between ages ${}_0t_{\rho'}$ and t_λ after any period ϕ has elapsed during the *first year* following an increase in mesh size, provided $\phi < v$, is

$$R'e^{-M\phi}\sum_{p=0}^{V-1} e^{-(F_0 + M)p} + R'e^{-(F_0 + M)V - M\phi} + R'e^{-(F_1 + M)\phi}\sum_{p=V+1}^{\lambda_0 - 1} e^{-(F_0 + M)p} \quad .. \quad (8.26)$$

Unless $V = o$, the first term of (8.26) refers to fish between ages ${}_0t_{\rho'}$ and ${}_1t_{\rho'}$, which although previously part of the exploited phase do not now enter the new exploited phase during the first year. The second term refers to the 'intermediate' year-class, one year older than the oldest in the first term, which will enter the exploited phase later in this first year, i.e. when $v \leqslant \phi < 1$. The last term denotes those age-groups within the new exploited phase, which are therefore fished both before and after the mesh change. Later in the first year, when $\phi \geqslant v$, the intermediate year-class will enter the new exploited phase, and the number present will be

$$R'e^{-M\phi}\sum_{p=0}^{V-1} e^{-(F_0 + M)p} + R'e^{-(F_0 + M)V - M\phi - (F_1 + M)(\phi - v)} +$$

$$+ R'e^{-(F_1 + M)\phi}\sum_{p=V+1}^{\lambda_0 - 1} e^{-(F_0 + M)p} \quad .. \quad .. \quad .. \quad (8.27)$$

To obtain the yield during the first year we introduce the parameters of growth and integrate with respect to ϕ the terms containing F_1 in (8.26) and (8.27); the limits being 0 to v for (8.26) and v to 1 for (8.27). Performing the summations gives

$$ {}_1Y_W = A\sum_{n=0}^{3} B_n \left\{ e^{-\alpha V - \delta v}\left(1 - e^{-\beta(1-v)}\right) + \frac{1-e^{-\beta}}{1-e^{-\alpha}}\left(e^{-\alpha(V+1)} - e^{-\alpha\lambda_0}\right)\right\} \quad .. \ (8.28) $$

It will be noted that (8.27) (and hence (8.28)) will hold for any value of V providing the first summation term of (8.27) is put to zero if $V = 0$. For the second and subsequent years of the transitional phase it is no longer possible to obtain a single expression which will hold for all values of V, and we restrict discussion to the two most likely cases, namely $V = 0$ and $V = 1$.

If $V = 0$, the yield in any year of the transitional phase is given by an expression exactly analogous to (8.28), and for the year X, where $1 \leqslant X \leqslant \lambda_0 - 1$, we have

$$ = A\sum_{n=0}^{3} B_n \left\{ e^{-\delta v}\left(1 - e^{-\beta(X-v)}\right) + \frac{e^{-\beta(X-1)}(1-e^{-\beta})}{1-e^{-\alpha}}\left(e^{-\alpha} - e^{-\alpha(\lambda_0 - X + 1)}\right)\right\} $$

$$ .. \quad .. \quad (8.29) $$

If $V = 1$, although the yield in the first transitional year is given by (8.28) as before, those for the second and subsequent years contain terms not present in (8.28). To develop the required expression we must again express the number present after a period ϕ where $\phi \geqslant v$. Thus for the second transitional year, i.e. for $X = 2$, we have

$$ R'e^{-M\phi} + R'e^{-M(1+\phi) - F_1(\phi - v)} + R'e^{-2M - F_0 - F_1(1-v) - (F_1+M)\phi} + $$

$$ + R'e^{-(F_1+M)(1+\phi)} \sum_{p=2}^{\lambda_0 - 2} e^{-(F_0+M)p} $$

while for years $X = 3$ to $X = \lambda_0 - 2$ inclusive, we have

$$ R'e^{-M\phi} + R'e^{-M(1+\phi) - F_1(\phi - v)} + R'e^{-2M - F_1(1-v) - (F_1+M)\phi} \sum_{=0}^{X-3} e^{-(F_1+M)p} + $$

$$ + R'e^{-2M - F_0 - F_1(1-v) - (F_1+M)(X-2) - (F_1+M)\phi} + R'e^{-(F_1+M)(X-1+\phi)} \sum_{p=2}^{\lambda_0 - X} e^{-(F_0+M)p} $$

$$ .. \quad .. \quad (8.30) $$

For the last transitional years, $X = \lambda_0 - 1$, the last term of (8.30) disappears, but otherwise the expression for the number present is the same. Although these expressions differ to some extent it is found that the yield for all years between $X = 2$ and $X = \lambda_0 - 1$ can be expressed by a general equation, viz.:

$$ {}_XY_W = A\sum_{n=0}^{3} B_n \left[e^{-\delta(1+v)}\left\{1 - e^{-\beta(X-1-v)} + e^{-\beta(X-2-v)-\gamma}\left(1 - e^{-\beta}\right)\right\} + \right. $$

$$ \left. + \frac{e^{-\beta(X-1)}}{1-e^{-\alpha}}\left(e^{-2\alpha} - e^{-\alpha(\lambda_0 - X + 1)}\right)\left(1 - e^{-\beta}\right)\right] \quad .. \quad (8.31) $$

It will be seen that putting $X = \lambda_0 - 1$ in (8.31) results in the last term becoming zero, as required.

Expressions for other characteristics of the catch and population during the transitional phase following a change in mesh size can be obtained by similar methods [cf. (8.23), (8.24) and (8.25)], though special care is needed when evaluating the new pre-exploited phase of the population, since, unlike the effect of a change in fishing mortality only, the numbers and biomass of this phase will vary during the transitional period.

It may be noted that if, in a particular case, an increase in mesh size does not affect the efficiency of the gear, or if the fishing intensity is changed simultaneously so as to compensate for any change in the efficiency of the gear, we have $F_0 = F_1$, and hence

$$\alpha = \beta$$

and

$$\gamma = (2F_0 + M + nK)$$

Making these substitutions in the above equations gives the expressions required.

8.3 Some Problems Concerning the Relationship between Fishing Mortality and Fishing Intensity

To conclude this discussion of problems raised by the characteristics of the fishing mortality we comment briefly on three matters which are not conveniently included in the foregoing parts of §8. The first of these concerns the fundamental relationship between fishing intensity and the resulting fishing mortality, which has a bearing on the representation of fishing mortality in fisheries operating in restricted areas such as rivers, and on the estimation of mortality parameters from data. In §8.3.2 we discuss possible ways in which that relationship might be affected by population density, and finally, in §8.3.3 consider some of the problems raised when the fishing intensity varies during the year, an extreme case of which is that of fishing being sharply restricted to a fishing season.

8.3.1 *Fundamental properties of competitive and non-competitive fisheries*

When first discussing the mathematical representation of the fishing mortality as an exponential coefficient in §3.3 we mentioned that such a coefficient could be regarded for most practical purposes as being proportional to the fishing intensity, the latter being measured as the total time spent fishing by vessels per unit time and area. In what follows we attempt to establish a more exact relationship between these quantities.

Baranov (1918) has discussed this problem from the point of view of establishing the relationship between the proportion of the exploited area swept by the gear during the course of the year and the resulting fishing mortality coefficient. Ricker (1940) adopts a different approach, which is to establish the relationship between fishing effort and the 'annual fishing mortality', m, and also the 'rate of exploitation', μ. Since, in his use, m has no meaning unless natural mortality is zero, and μ contains the natural mortality rate, the usefulness of this approach is limited; the method also leads to a complicated terminology that has resulted in some confusion (see, e.g. Schaefer, 1943).* It therefore seems necessary to re-emphasize the importance and essential simplicity of the relationship between fishing effort and the instantaneous fishing mortality coefficient F, especially as Ricker (1940, p. 60) has criticised its usefulness in practice. For this purpose we shall extend the methods used by Baranov which are similar in principle to those recently applied to the problem of animal trapping by Moran (1951).

We begin by considering a simple case of one ship fishing an area containing a uniformly distributed population in which there is no natural mortality or recruitment. We suppose that the ship is using a gear such as the trawl which can be regarded as catching during each haul a certain proportion of the fish in its path. Now we can suppose that at the beginning of a certain haul the number of fish in the whole population is N, so that as a result of this first haul a certain proportion p of the total population is removed, pN in number. The number of fish remaining is qN, where $q = 1 - p$, and for the moment we assume that these redistribute themselves over the exploited area between the end of the first haul and the beginning of the next. The second haul will again catch the proportion p of the number present, i.e. qN, so that the number caught in the second haul is pqN and the number remaining q^2N. Thus in the rth of such hauls the number caught will be $pq^{r-1}N$ and the number remaining after the rth haul will be q^rN. If each haul is of the same duration and is made with gear of a given efficiency, p and q will be constants; we therefore put

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*The use of annual mortality rates raises the problem of 'competition' between different causes of mortality, which is also encountered in the interpretation of bio-assay data. In that field the expression used by Ricker to relate percentage survivals and instantaneous coefficients of mortality is known as Abbott's correction for mortality in the control, a useful table of which is given by Healy (1952).

$$q = e^{-a}$$

where a is a constant. Then

$$q^r = e^{-ar}$$

Now we can specify r as having any value, and if we wish we can regard it as a constant. Putting

$$ar = u$$

we have

$$q = e^{-u/r}$$

and in the limit, as $u/r \to 0$, $q \to 1-u/r$, so that when u/r is very small

$$1 - q = p \simeq \frac{u}{r} \qquad \ldots \quad \ldots \quad \ldots \quad (8.32)$$

The number of fish caught during the first haul was pN; if we regard this haul as occupying an extremely short time relative to the period during which the total number of hauls, r, is made, then the instantaneous rate of decrease of the population at the time when the first haul was made can be written as

$$_F\left(\frac{dN}{dt}\right) = -pN \simeq -\frac{u}{r}N$$

So far we have supposed that the population is being fished by a single vessel, but we can now extend the above treatment to the case in which any number of vessels, n, are fishing simultaneously and using gear of the same efficiency. Since we are supposing that there is no redistribution of fish while each haul is in progress, it follows that the number of fish caught in a haul by any one vessel is not influenced by the catches of any other vessels during the time occupied by that haul. The total number of fish caught during the n hauls in progress at any given time will be npN, and we have

$$_F\left(\frac{dN}{dt}\right) = -npN \simeq -\frac{nu}{r}N \qquad \ldots \quad \ldots \quad \ldots \quad (8.33)$$

But for fishing gear of a given efficiency, a fleet of a given size, and with the value of r specified (this might be the total number of hauls made by a vessel in a given period of time such as a year) the quantity nu/r is constant and we may replace it by a single constant, say

$$\frac{nu}{r} = F \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (8.34)$$

Then the total instantaneous rate of decrease of the population due to the activity of the whole fleet becomes

$$_F\left(\frac{dN}{dt}\right) \simeq -FN$$

which is identical to (3.2) which we have used to represent the rate of decrease in numbers due to fishing throughout this paper, and F is, in fact, the instantaneous fishing mortality coefficient.

Now it will be noted that this proportional relationship between F and fishing intensity depends upon the approximation introduced to obtain (8.32), namely that p can be regarded as being extremely small. Strictly we should write

$$e^{-u/r} = 1 - p$$

from which

$$F = -n \log (1 - p) \qquad \ldots \qquad \ldots \qquad \ldots \qquad (8.35)$$

Hence we find that although F is still proportional to the total number of vessels, it is logarithmically related to the fishing power of each vessel and gear. The value of p has to be relatively large before the quantity—log $(1 - p)$ differs appreciably from p; for this difference to amount to 1%, for example, p must be about 0.02, and in deep-sea fisheries it will usually be much smaller than this.

The theoretical model developed above contains certain simplifying assumptions which we must now examine further. The assumption that there is no natural mortality or recruitment does not influence the generality of the conclusions, since the natural mortality rate as an instantaneous coefficient can be included in (8.33) by direct addition, and the question of recruitment does not arise if we measure mortality in terms of the decrease in numbers of a given batch of fish—as is indeed the procedure necessary in practice. The assumptions that require further mention are that redistribution is restricted to the inter-haul period and is then perfect, and that fish are uniformly distributed.

In a large deep-sea fishery the process of redistribution is relatively slow; hence the density of fish in the vicinity of any given vessel is scarcely influenced by the magnitude and distribution of the *contemporary* fishing activity—as it would if redistribution was rapid—but depends on the fishing during a certain preceding interval of time, and the slower the rate of redistribution the longer is this period. One consequence is that the process of redistribution is not restricted to the inter-haul period—which in any case is usually shorter than the duration of the haul—so that the effects of a proportionate change in the number of vessels or the fishing power of each are even more similar than those predicted by (8.35).

When fish are not uniformly distributed, the proportion of the whole population taken in each haul (i.e. the value of p) is not constant but depends on the local density of fish, and a haul made where the density is high causes a greater mortality than one where the density is low. In these circumstances it is necessary to sub-divide the exploited area into smaller areas within each of which the density is sufficiently uniform that the value of p can be regarded as constant. In each of these sub-areas the fishing intensity is proportional to the fishing mortality coefficient, though the constant of proportionality is different in each. Hence an index of total fishing intensity for the whole area that is proportional to the total mortality coefficient must be a weighted sum of the intensities in each sub-area taking the local density of fish into account. This index we call the *effective overall fishing intensity*, $\bar{f}$, and its determination from data is discussed in more detail in §10.2.3. It should be noted, however, that if the relative distribution of fish and fishing remains fairly constant the unweighted average value of p is also constant; in these circumstances the total fishing mortality coefficient can be therefore taken as roughly proportional to the total fishing effort, as would be theoretically true if fish were uniformly distributed.

It will be realised that the fishery we have been discussing is a competitive one, in that the rate at which any given vessel is catching fish at any moment is partly dependent on how much has previously been caught by the fleet as a whole, including the vessel in question. The term *interactive fishing* might be used to embrace both strictly competitive fishing of this kind, and also instances in which the catches of certain fishing units are influenced by the previous catches of other units, but in which the converse is not true. Such a case of one-way interaction may be used to illustrate the fundamental difference between interactive and non-interactive fishing. Consider a simplified river fishery based on an anadromous species, in which fish 'run the gauntlet' of successive units of gear in progressing from the mouth of the river to the spawning area at the head. To obtain a fully interactive fishery in this case we need to have the units of gear arranged along one bank, as shown in Fig. 8.5.1, and suppose that each removes a proportion p of fish which pass it on their way upstream.

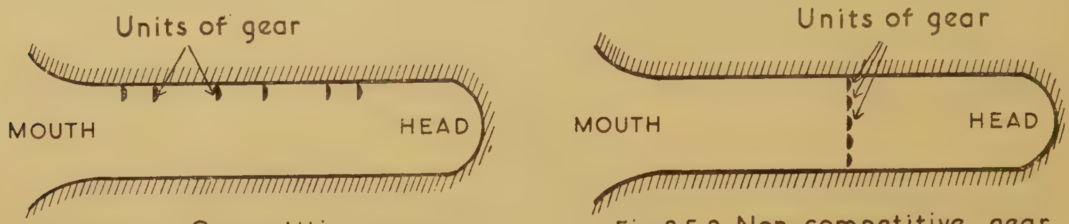

Fig. 8.5.1 Competitive gear

Fig. 8.5.2 Non-competitive gear

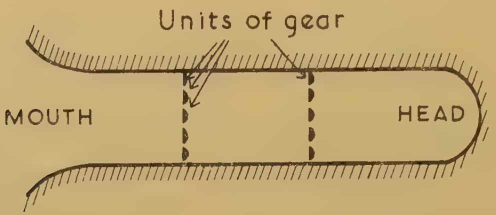

Fig. 8.5.3 Competitive & non-competitive gear

FIGS. 8.5 EXAMPLES OF INTERACTION BETWEEN FISHING UNITS

[The difference is shown diagrammatically by taking a highly simplified example of a river fishery based on an anadromous species. Fish are assumed to progress steadily from the mouth of the river to its head, encountering *en route* units of gear arranged along the banks (interacting) or transversely across the river (not interacting and therefore non-competitive).]

Let us suppose that a number of fish dN enter the river during a short period of time, so that the number caught by the first unit of gear encountered will be $p.dN$. If we denote the natural mortality by a constant exponential coefficient M, and suppose that the survivors redistribute across the river, then the number reaching the second unit of gear will be $p.dNe^{-Mt_{12}}$, where t_{12} denotes the time taken by the fish to pass from the first to the second unit. Thus the catch of the second unit of gear will be

$$pq.dNe^{-Mt_{12}}$$

and the number reaching the third unit will be

$$q^2 . dNe^{-M(t_{12}+t_{23})}$$

The number reaching the spawning ground after encountering a total of r units of gear during a period of time τ after entering the river will be

$$q^r . dNe^{-M\tau}$$

and the total number of fish entering the river during the whole season will be

$$\int_{T_1}^{T_2} \frac{dN}{dt}\, dt = N_1$$

where T_1 and T_2 are the dates on which the run begins and ends respectively.* Hence the total number of fish reaching the spawning area will be

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*The fact that the form of the function dN/dt does not need to be specified is important. Thus in all the population models developed in this paper we have supposed that recruitment occurs instantaneously each year, but the equations for a population in a steady state would be the same if the entry of recruits took any function of time—provided this remains unchanged—including the opposite extreme of recruitment occurring at a constant rate throughout the year, as postulated by Baranov (1918) (see §4.2).

$$N_2 = N_1 q^r e^{-M\tau}$$

from which, remembering that $q = 1 - p$, we have

$$\frac{1}{\tau} \log \frac{N_1}{N_2} = -\frac{r}{\tau} \log (1 - p) + M \quad \ldots \quad \ldots \quad (8.36)$$

so that for this interactive fishery we find that the instantaneous total mortality coefficient [i.e. $(1/\tau) \log (N_1/N_2)$] is linearly related to the total number of units of gear. This relationship is of fundamental importance and will be used in §14.3 as the basis for a method of estimating separately the natural and fishing mortality coefficients in the case of a deep-sea fishery. If p is sufficiently small we can write (8.36) in the form

$$\frac{1}{\tau} \log \frac{N_1}{N_2} \simeq \frac{rp}{\tau} + M \quad \ldots \quad \ldots \quad \ldots \quad (8.37)$$

so that changing either the number of units of gear or the fishing power of each alters the slope of the regression only. If the units of gear all have the same fishing power and are distributed evenly along the river the equation for yield in numbers from this interactive fishery is identical with (5.9). If these conditions are not satisfied, (8.37) will still give the correct relationship for the mortality rate, but the yield will now depend on how the units of gear are distributed. To take such complications into account it may be necessary to write the yield in a form such as

$$Y_N = N_1 \sum_{u=1}^{r} p_u \prod_{s=1}^{u-1} \left(1 - p_s\right) e^{-M \sum_{s=1}^{u-1} t_s}$$

where p_u is the fishing power of the uth unit of gear and t_u is the time taken by fish to pass from the uth to the $(u + 1)$th unit.

Now let us see the consequences of supposing that there is no interaction between units of gear, for which purpose we can regard the latter as being arranged in a line across the river at one point, as in Fig. 8.5.2, and postulate that a total of N_1 fish reach the gear during the season. Then if each unit of gear removes the proportion p of all fish passing it, the total number caught will be rpN_1 and the number reaching the spawning ground will be given by

$$N_2 = N_1 (1 - rp) e^{-M\tau}$$

where τ is now the time taken by fish to pass from the place at which the gear is set to the spawning ground. Thus for a non-interactive and therefore non-competitive fishery we find

$$\frac{1}{\tau} \log \frac{N_1}{N_2} = -\frac{1}{\tau} \log \left(1 - rp\right) + M \quad \ldots \quad \ldots \quad \ldots \quad (8.38)$$

Although p may be small the product rp may well not be, and in general it will not be possible to approximate to $-\log (1 - rp)$ by writing rp. Thus in a non-competitive fishery we find that the relationship between total mortality coefficient and fishing effort is not linear. Furthermore, the yield is now

$$Y_N = rpN_1$$

and the natural mortality is relevant only in so far as it is the cause of reduction in the number of fish while they are proceeding from the mouth of the river to the place at which the gear is set.

In practice we should usually find that river fisheries contain both interactive and non-interactive features. Thus units of gear may be arranged along both banks or across the river at a number of points, as in Fig. 8.5.3. Let us suppose that the total of r units of gear are to be arranged in x sets between which there is interaction, but that the r/x units of gear within each set do not interact with each other. By the above methods we have

$$N_2 = N_1 \left(1 - \frac{r}{x} p\right)^x e^{-M\tau}$$

from which

$$\frac{1}{\tau} \log \frac{N_1}{N_2} = -\frac{x}{\tau} \log \left(1 - \frac{r}{x} p\right) + M \qquad \ldots \quad \ldots \quad (8.39)$$

It can now be seen that a linear relationship between total mortality coefficient and fishing effort will be found only if changes in the number of units of gear are the result of increasing the number of sets, i.e. if r/x is constant; if any change in the number of units per set occurs, the relationship will not be linear. For example, Thompson (1945), in an analysis of the Fraser river fishery for sockeye salmon, appreciated that this fishery may not be a truly competitive one, and gave alternative assessments according to whether it was assumed that the fishery was wholly competitive or wholly non-competitive. With the above methods, however, it is possible to distinguish between these alternatives, and we shall show in §14.3.2.2 that for practical purposes the Fraser river fishery is a competitive one.

8.3.2 *Dependence of the fishing mortality coefficient on population density—gear saturation*

The next question to consider is what may be described as the variation of the fishing mortality coefficient with population density. Now unlike the parameters of recruitment, natural mortality and growth, the fishing mortality coefficient is a parameter the magnitude of which we are supposing can be specified as having any desired value. One purpose of this paper is, in fact, to provide means for assessing the probable state of a fish population corresponding to any given value of the fishing mortality coefficient, so that to speak of a variation in the magnitude of this parameter with population density is, to this extent, meaningless. On the other hand a given fishing mortality coefficient must be achieved, in practice, by means of a certain fishing effort, and if it should happen that the mortality caused by that effort is influenced by population density, the effect would be analogous to a variation with density of the fishing mortality coefficient itself. In such cases we cannot treat F as an independent variable, and the problem is one of investigating ways in which variations in density can influence the relationship between fishing mortality coefficient and fishing effort. These have been cited by Ricker (1940) as factors that may cause the properties of real fisheries to depart from those predicted by simple theoretical models.

One way in which density can influence the total mortality coefficient generated by a given effort arises from non-uniform distribution of fish and effort and has been touched on in the previous section. Thus if an increase in the total abundance of a fish population should enable the fleet to concentrate more effectively on the highest densities of fish, the same effort would generate a higher fishing mortality coefficient. Analysis of this factor involves a study of the process of *fish searching* and is discussed in §10.3; here we are concerned with the effect of fish density on the fishing power of individual vessels or units of gear, and is what we shall term *gear saturation*. By this is meant the tendency for the fishing power of a unit of gear to become reduced as the catch in it increases. It is possible, for example, that the presence of a large amount of fish in a trawl reduces its catching power, while the extremely heavy cod fishing that is sometimes encountered in Arctic waters may cause the net to burst, with the loss of the entire catch. Sustained heavy catches may also result in a vessel having temporarily to cease fishing in order to clear decks, though this is taken into account if fishing intensity is measured in terms of actual fishing time. If such a fishery is regulated by fixing the number of vessels it would be necessary to take account of the fact that with fewer vessels operating on a more abundant stock their actual fishing time might decrease owing to greater or more frequent saturation.

Saturation may be more pronounced with other types of gear such as the drift net, where a concentrated shoal may encounter a relatively small section of the net within a short time so that the bulk of the shoal cannot be captured. It is not necessary in this case that saturation should mean that all available meshes contain a fish, since the presence of the first to be captured may scare the remainder and cause them to swim above or below the net. Perhaps the gear most likely to become saturated is the long-line, since the number of fish in a dense shoal encountering it may far exceed the number of hooks available for their capture, and the fishing power of a unit of such gear varies directly with the number of unoccupied hooks. If an analysis is attempted of a fishery in which gear saturation is appreciable, its consequences will be far-reaching. For example, the catch per unit effort will not increase proportionately with the abundance of fish but will tend to a limit; thus this quantity will not provide a reliable measure of abundance and cannot be used to estimate mortality rates. In such a case it would be necessary by means of gear experiments to obtain true indices of abundance, e.g. by using a different type of gear not liable to be saturated, with which may be compared the observed abundance; it might then be possible to deduce correction factors to adjust the commercial statistics of catch and effort. Alternatively, saturation effects may be measured by carrying out, on various densities of fish, comparative fishing experiments in which the time that the net is down, instead of the type of gear, is varied; data of this kind for gill nets have been given, for example, by Kennedy (1951). Provided the accumulation of captured or dead fish in the net does not scare away newcomers, it would seem reasonable to assume in such a case that the rate of capture is approximately proportional to the vacant area of the net, as well as to the abundance of fish. Then the catch per net, c, would be related to the interval between lifts (i.e. the fishing time or duration of haul), τ, by an expression of the type

$$c = c_{\infty}(1 - e^{-A\tau}) \quad \dots \quad \dots \quad \dots \quad (8.40)$$

where c_{∞} is a constant and A a parameter proportional to the absolute abundance of fish (Kennedy's 'availability'). Estimates of both c_{∞} and A can be obtained if the catches resulting from two or more intervals between lifts are known. The above equation gives saturation curves with characteristics similar to those drawn freehand by Kennedy, and provides immediately a means of correcting catch per unit effort data for this effect. Gear saturation, however, is not likely to be appreciable in the North Sea trawl fisheries where the large catches which might be expected to reduce the fishing power of a trawl of the size in common use are seldom taken. Certainly, we know of no data indicating the existence of this effect in these fisheries, and we shall not attempt a more detailed analysis here. It may be noted that Kesteven's (1946) treatment of fishing mortality implies that the catch is unrelated to the abundance of the fish population, which is essentially the condition that would be found if the gear were always completely saturated before being hauled in. Gulland (1955 a) has also discussed the theoretical consequences of gear saturation, and has developed an expression from which the effective fishing power of a unit haul of a gear can be determined from a knowledge of the actual catch of that haul in relation to the saturation catch.

8.3.3 *Seasonal variations in fishing intensity*

We have not dealt in detail with the seasonal variation of parameters (i.e. variation during the course of the year) since for the most part it is not likely to be of importance from the point of view of the long-term behaviour of a population. Thus we mentioned in §8.3.1 that virtually the same equilibrium yield is obtained whether recruitment occurs instantaneously, at a constant rate throughout the year, or as any function of time—with a periodicity of one year. Again, it is usually sufficient with continuous fishing to assume that growth is uniform during the year (i.e. is described by constant values of the parameters K and W_{∞}). The situation in which it may be essential to take account of the seasonal variation of parameters is when fishing activity is completely restricted to a fishing season appreciably less than a year in duration, especially if this restriction is the result of legislation and assessments are based on a study of the fishery when it was continuous. It is not possible to deal with this case in any detail, since the consequences depend on a number of factors such as the time relations between the fishing season and the growth and recruitment seasons. The rate of movement of fish may also be important, since if the fishing season is short there may not be time for the spatial distribution of the fish to become steady.

There is one factor, however, that has been considered by Ricker (1944) and which needs further comment, namely the interaction between fishing and natural mortalities when fishing is restricted to a particular season. To take an extreme case we may suppose that recruitment occurs effectively instantaneously at the beginning of the fishing season, and that the natural mortality rate is constant; if the fishing season lasts for the fraction v of a year, then by methods analogous to those of §8.2 the equilibrium seasonal yield in numbers is given by

$$ {}_vY_N = \frac{FR'}{F+M}\left(1 - e^{-(F+M)v}\right)\left(\frac{1 - e^{-(vF+M)\lambda}}{1 - e^{-(vF+M)}}\right) \quad \ldots \quad \ldots \quad (8.41) $$

If, however, we were to approximate to (8.41) by using (5.9) for a non-seasonal fishery and suppose that the same fishing effort was distributed throughout the year, we should have

$$ {}_vY'_N = \frac{vFR'}{vF+M}\left(1 - e^{-(vF+M)\lambda}\right) \quad \ldots \quad \ldots \quad (8.42) $$

The error involved by using (8.42) instead of (8.41) is therefore given by the extent to which the expression

$$ \frac{Y_{Nv}}{{}_vY'_N} = \frac{F(vF+M)}{vF(F+M)} \cdot \frac{\left(1 - e^{-(F+M)v}\right)}{\left(1 - e^{-(vF+M)}\right)} \quad \ldots \quad \ldots \quad (8.43) $$

differs from unity. This expression is always greater than unity if M is finite, so that (8.42) gives an underestimate of the true yield, but the particular value of (8.43) depends on those of v, F and M. It can be seen, however, that

(i) As $v \to 1$, (8.43) $\to 1$

(ii) As $v \to 0$, (8.43) $\to \dfrac{M}{1 - e^{-M}}$

(iii) As $M \to 0$, (8.43) $\to 1$ for any value of v

(iv) For a given value of v, (8.43) increases as M increases.

SECTION 9: GROWTH AND FEEDING

Hitherto, we have referred to a constant growth pattern; that is, we have taken the change of weight of the organism with age to follow a prescribed pattern defined by a mathematical expression the parameters of which have constant values. In this section we are concerned with the variation of growth (i.e. in the pattern of variation of weight with age) with age itself (§9.2), among the individuals comprising a given year-class (§9.3) and with population density and the supply of food (§9.4). We shall represent these variations by appropriate changes in the values of the parameters of the von Bertalanffy growth equation.

The reasons why we have used the von Bertalanffy equation in the population models developed in this paper were mentioned in §3.4. Briefly, they are that the equation gives a satisfactory representation of the growth of fish, that it is based on physiological concepts and hence can be used to investigate problems such as the variation of growth with food supply, and that its incorporation into theoretical population models presents no mathematical obstacles. At this point we need to substantiate these reasons for our choice by reviewing briefly the claims of certain other well-known growth equations.

9.1 GROWTH EQUATIONS OTHER THAN THAT OF VON BERTALANFFY

When considering the choice of a mathematical expression for growth for use in a theoretical population model we must decide at the outset whether we are to regard the expression as a purely empirical representation of weight-at-age or whether we wish to attach biological significance to the parameters it contains. The evidence from a great number of studies on many different kinds of animals indicates that despite complicating factors—varying environmental conditions, physiological influences such as the onset of maturity—there is nevertheless an underlying pattern of growth which is remarkably consistent in its occurrence. Typically, growth in the linear dimension follows a curve which is concave downwards and which approaches an asymptotic value as age increases. Since the weight of a fish is usually approximately proportional to the cube of the linear dimension—and often very closely so—we find that growth in weight is typically an S-shaped curve which also approaches a limiting value. A fairly general feature of this latter curve is that it is not symmetrical, the inflection usually occurring at a weight less than half the asymptotic weight. The generality and simplicity of this growth pattern suggests that there might be certain basic growth laws common to many animals and which could be given a rational formulation by mathematical means. It will be noted in this connection that it is a necessary, but not a sufficient, requirement of a mathematical growth expression of this kind that it should represent adequately the basic pattern of growth as defined above.* The fact that the closeness of fit of a theoretical equation to observed data is not in itself sufficient to establish the interpretation of the parameters involved was pointed out by Gray (1929) and has been elegantly demonstrated by Kavanagh and Richards (1934). In the present connection it is necessary also that the implications of any mathematical expression should conform, at least in a general sense, to what is known of the physiology of growth.

9.1.1 *Review of some published growth equations*

Ottestad (1933) was impressed by the immense complexity of the processes concerned in growth, and suggested that the summation of them as a function of time would be analogous to the ogive of a normal frequency distribution. This method fails partly because it produces a symmetrical ogive and also because it does not seem satisfactory to regard growth as the net result of many factors acting independently and randomly.

The Gompertz equation, originally developed by Gompertz (1825) in connection with the analysis of mortality in humans, has been applied on a number of occasions to the growth of organisms and has been given a physiological interpretation by Weymouth, McMillin and Rich (1931). The concept put forward by these authors is in effect that growth is an additive process which is continuously slowing down. They were concerned primarily with growth in length of certain mollusca and found from their data that the logarithm of the relative growth in length decreased approximately linearly with age, i.e.,

$$\log\left(\frac{1}{l}\cdot\frac{dl}{dt}\right) = a - kt$$

which, on integration, gives the Gompertz equation

$$l_t = be^{-(1/k)e^{a-kt}} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (9.1)$$

The authors do not attempt a physiological interpretation of any of the three coefficients and it is difficult to escape the conclusion that the basis of this equation is largely empirical. From the physiological point of view there is abundant evidence that growth is not merely additive but that breakdown of body material must be taken into account as well. Further,

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*For this reason we have not discussed certain growth equations that do not give an inflection in the curve of weight against age. These include Glaser's (1938), Schmalhausen's (1927, 1931) and the simple exponential (see, e.g. Ricker (1944)).

(9.1) has an inflexion; but this is not a feature of many curves of growth in *length*, a point which seems to have been overlooked by these authors in their review of the significance of an inflection in the growth of animals. It is true that fitting it to their data gives an inflection, but this is so near to the origin that it could very easily be due to a qualitative change in the growth pattern rather than confirmation of the applicability of (9.1), since it could scarcely be expected that growth during very early life would conform to the adult pattern.

The concept of growth as the resultant of processes tending to increase the weight of an animal and those tending to decrease it, which we found to be absent from the interpretation of the Gompertz equation discussed above, will be recognized as an essential feature of the von Bertalanffy equation. The same concept appears in other formulations of growth, one of which is that of Brody (1945). Brody regards the portion of the curve of growth in weight from the origin to the point of inflection as the self-accelerating phase, for which he writes

$$\frac{dw}{dt} = kw$$

giving

$$w_t = Ae^{-kt}$$

while that between the inflection and the asymptote he terms the self-inhibiting phase, expressed by the equation

$$\frac{dw}{dt} = k(A - w)$$

of which the solution is

$$w_t = A - Be^{-kt}$$

These expressions give a good representation of data of weight-at-age, though this is partly due to the freedom with which the exact position of the inflection can be chosen. However, the implication that there is a qualitative change in the growth processes at the inflection is not substantiated from physiological experience, as has been pointed out by several authors; rather, the evidence suggests that the accelerating and inhibiting processes are present in all phases of growth.

The autocatalytic or logistic equation developed by Robertson (1923) satisfies this particular requirement since it combines, in effect, both of Brody's phases in one equation. Thus the autocatalytic equation is

$$\frac{dw}{dt} = kw(A - w) \quad \ldots \quad (9.2)$$

having the solution

$$w_t = \frac{A}{1 + e^{-Akt}} \quad \ldots \quad (9.3)$$

When the two processes are combined in this way the resulting equation (9.3) gives a symmetrical sigmoid curve for growth in weight and does not therefore give a satisfactory representation of the observed facts. Brody's procedure of separating the processes avoids this difficulty but would seem unacceptable on physiological grounds, and attempts by other authors to introduce asymmetry into (9.3) are unsatisfactory for a similar reason. Thus Pearl and Reed (1923) modified (9.3) by introducing a polynomial in t in the exponent, i.e. they wrote

$$w_t = \frac{A}{1 + be^{-(k_0 + k_1t + k_2t^2 + \ldots\ldots\ldots\ldots k_nt^n)}}$$

This produces the required asymmetry but renders the equation largely empirical.

By multiplying out the right hand side of (9.2) the autocatalytic equation can be written as

$$\frac{dw}{dt} = Akw - kw^2 \quad \ldots \quad \ldots \quad \ldots \quad (9.4)$$

In this form it can be seen that the equation implies that the processes tending to increase the weight of the organism are a function of the weight itself, while those tending to decrease weight proceed at a rate proportional to its square. When this equation is applied to the growth of a population in numbers, i.e.

$$\frac{dn}{dt} = Akn - kn^2$$

the term kn^2 can be interpreted as referring to the interaction between individuals (see Kostitzin, 1939, p. 57), but there seems to be no analogous process in the growth of an organism. Von Bertalanffy's equation, using the above terminology, is

$$\frac{dw}{dt} = Akw^{2/3} - kw$$

which is seen to be similar to (9.4) except that the catabolic processes are represented as a rate proportional to weight itself instead of to its square, and the anabolic processes at a rate proportional to the two-thirds power of weight (i.e. the 'physiological surface area') instead of to weight itself. As well as obtaining by this means an equation that gives an asymmetrical sigmoid curve of growth without the introduction of any empirical modifications, von Bertalanffy has shown that there is abundant physiological evidence to support his representation of the anabolic and catabolic processes. Some mention of this is made where relevant in this paper (e.g. §9.4), but for a more complete account we would refer the reader to von Bertalanffy (1949). The closeness with which von Bertalanffy's equation fits growth data of fish is demonstrated in §16.2.

9.1.2 *A simple population model using a polynomial growth equation*

Although we are of the opinion that von Bertalanffy's growth equation is the most satisfactory of any that have hitherto been developed, it is important to note that the validity of the population models of Part I, in which the growth pattern is assumed constant, does not depend specifically on its use. Moreover, it may well be that in certain cases there are departures in detail from the generalised pattern of growth which we have outlined. For example, there may be large variations in the quality or abundance of food available to fish of different ages which introduce distortion in the shape of the growth curve. If this distortion is appreciable it may not be satisfactory to use the von Bertalanffy equation, but any expression that fits adequately the weight-at-age data for the species in question can be incorporated in the simple population models. It must be remembered, however, that with an empirical approach of this kind it is not possible to extrapolate beyond the range of the data nor to use the model to predict the effects of phenomena such as variation of growth with density.

To show the form taken by the simple population models in such a case, we use as an example a polynomial expression for weight as a function of age, viz.:

$$w_t = a_0 + a_1 t + a_2 t^2 + \ldots . \, a_x t^x \ldots . \, a_r t^r$$

$$= \sum_{x=0}^{r} a_x t^x \; .$$

Such an expression could be fitted to data by the usual methods, using as large a value of

r as is necessary to obtain an adequate fit. Putting

$$t - t_{\rho'} = \psi$$

we have the annual yield in weight given by

$$Y_W = FRe^{-M\rho}\sum_{x=0}^{r} a_x \int_0^{\lambda} \psi^x e^{-(F+M)\psi} d\psi$$

To integrate,* it is first necessary to establish a reduction formula for the expression

$$I_x = \int_0^{\lambda} \psi^x e^{-(F+M)\psi} d\psi$$

which is

$$I_x = -\left[\frac{\psi^x}{F+M} e^{-(F+M)\psi}\right]_0^{\lambda} + \frac{x}{F+M} . I_{x-1}$$

Substituting for I_{x-1} in terms of I_{x-2}, and for I_{x-2} in terms of I_{x-3}, etc., gives

$$I_x = \frac{1}{F+M}\left\{\frac{x\,!}{(F+M)^x} - e^{-(F+M)\lambda}\sum_{p=0}^{x}\frac{\lambda^{x-p} . x\,!}{(x-p)\,!\,(F+M)^p}\right\}$$

and hence

$$Y_W = FRe^{-M\rho}(a_0 I_0 + a_1 I_1 + \ldots . a_r I_r)$$

$$= FRe^{-M\rho}\sum_{x=0}^{r} a_x I_x$$

The annual yield is therefore given by

$$Y_W = \frac{FRe^{-M\rho}}{F+M}\sum_{x=0}^{r} a_x\left(\frac{x\,!}{(F+M)^x} - e^{-(F+M)\lambda}\sum_{p=0}^{x}\frac{\lambda^{x-p} . x\,!}{(x-p)\,!\,(F+M)^p}\right) \quad .. \quad (9.5)$$

It will be seen that using a linear increase of weight with age, i.e. putting $r = 1$ in (9.5), gives

$$Y_W = \frac{FRe^{-M\rho}}{F+M}\left\{a_0 + \frac{a_1}{F+M} - e^{-(F+M)\lambda}\left(a_0 + a_1\lambda + \frac{a_1}{F+M}\right)\right\}$$

which is the equation for yield given by Hulme, Beverton and Holt (1947). A linear growth in weight relationship has also been used by Doi (1951). Baranov's (1918) yield equation (10) can also be regarded as a special case of (9.5) in which $r = 3$ and $a_0 = a_1 = a_2 =$ zero. Another feature of Baranov's equation is that t_λ is put to infinity; this implies extrapolating an empirical growth equation beyond the range of the data and the consequences are discussed in §17.8.

9.2 VARIATION OF THE GROWTH PARAMETERS WITH AGE

It is found sometimes that discontinuities in the growth pattern occur at one or more stages in the life-history, the two most likely causes being; (a) the recruitment migration from nursery grounds to the main exploited area, with the result that recruits may commence feeding on a different type or abundance of food, and (b) the physiological changes resulting from the onset of maturity, a striking example of which in Lake Trout is given by Miller and Kennedy (1948). Since maturity may be attained during the exploited phase of the life-history, the problems raised by the two causes of discontinuity in growth are different, and are treated separately in §§9.2.1 and 9.2.2.

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*We must thank Dr. P. H. Thomas for help with the following integration.

9.2.1 *A break in growth pattern at recruitment*

The fact that there may be a sudden change in the growth pattern when recruitment to the exploited area occurs need be of limited significance only, since the von Bertalanffy equation is valid, and can be fitted to data, between any two ages. In such a case it could be fitted to weight-at-age data between ages t_ρ and t_λ, and the fact that it did not give a true representation of growth during the pre-recruit phase would be unimportant as far as the exploitation of the post-recruit phase is concerned. However, when investigating problems involving a change in growth that is restricted to the post-recruit phase of the population, as might result, for example, from a change in the abundance of that phase, fish would still enter the exploited area at the same weight and age and we may proceed by methods similar to those used in §9.3 when dealing with the differences in the growth rates of recruit sub-groups.

Let us suppose that we are dealing initially with an equilibrium population, the growth in the exploited phase of which can be described by the parameters ${}_1K$, ${}_1W_\infty$ and ${}_1t_0$, so that the weight at recruitment, W_ρ, is

$$W_\rho = {}_1W_\infty \sum_{n=0}^{3} \Omega_n e^{-n_1K(t_\rho - {}_1t_0)}$$

If now a change in the growth of the post-recruit phase takes place such that it can be described by values ${}_2K$ and ${}_2W_\infty$, the weight at any age t greater than t_ρ is given by the equation

$$w_t = {}_2W_\infty \sum_{n=0}^{3} \Omega_n e^{-n_2K(t - {}_2t_0)}$$

where

$${}_2t_0 = t_\rho + \frac{1}{{}_2K} \log \left\{ 1 - \left(\frac{W_\rho}{{}_2W_\infty} \right)^{1/3} \right\} \quad \ldots \quad \ldots \quad \ldots \quad (9.6)$$

in which t_ρ and W_ρ are constant by definition. Consequently, the mean weight at selection, $W_{\rho'}$, which is also a constant, can provide an expression for the corresponding mean selection age, viz.:

$${}_2t_{\rho'} = {}_2t_0 - \frac{1}{{}_2K} \log \left\{ 1 - \left(\frac{W_{\rho'}}{{}_2W_\infty} \right)^{1/3} \right\} \quad \ldots \quad \ldots \quad \ldots \quad (9.7)$$

so that the annual yield from the population, after the change in growth has occurred, is given by

$$Y_W = FRe^{-M({}_2t_{\rho'} - t_\rho)}{}_2W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-n_2K({}_2t_{\rho'} - {}_2t_0)}}{F + M + n_2K} \left(1 - e^{-(F + M + n_2K)(t_\lambda - {}_2t_{\rho'})} \right) \quad (9.8)$$

The converse situation is the occurrence of variations in the growth during the pre-recruit phase while the growth of the exploited phase remains constant, and we may distinguish two cases.

(i) If the recruitment migration takes place at a constant *weight*, W_ρ, the effect of a change in the pre-recruit growth will be that recruitment occurs at, say age ${}_2t_\rho$ instead of ${}_1t_\rho$. From the von Bertalanffy equation we may write

$$\rho = t_{\rho'} - t_\rho = \frac{1}{K} \log \left(\frac{W_\infty{}^{1/3} - W_\rho{}^{1/3}}{W_\infty{}^{1/3} - W_{\rho'}{}^{1/3}} \right)$$

see (9.6) and (9.7))

and since, for a given mesh size, $W_{\rho'}$ is constant, ρ is also constant. Again, the quantity

$$(t_{\rho'} - t_0) = -\frac{1}{K}\log\left\{1 - \left(\frac{W_{\rho'}}{W_\infty}\right)^{1/3}\right\} = \text{constant}$$

However, the duration of the pre-recruit phase will be longer or shorter according to whether ${}_2t_\rho$ is greater or less than ${}_1t_\rho$, so that the annual number of recruits will change to R_2 where

$$R_2 = R_1 e^{-M'({}_2t_\rho - {}_1t_\rho)}$$

the coefficient M' referring to the natural mortality rate during the period ${}_2t_\rho - {}_1t_\rho$, i.e. at the end of the pre-recruit phase. Finally, the fishable life-span will, strictly speaking, become

$${}_2\lambda = t_\lambda - {}_2t_{\rho'}$$

but this change can be neglected in the usual case in which λ is large. Consequently the equation for the equilibrium yield after the change in growth rate has taken place will differ from the original only in the annual number of recruits, and, in fact, we have

$$\frac{{}_2Y_W}{{}_1Y_W} = e^{-M'({}_2t_\rho - {}_1t_\rho)} = e^{-M'({}_2t_{\rho'} - {}_1t_{\rho'})} \quad \ldots \quad \ldots \quad (9.9)$$

(ii) If, on the other hand, recruitment occurs at a constant *age* t_ρ, a change in pre-recruit growth will result in fish migrating at weight ${}_2W_\rho$, say. The new age, ${}_2t_{\rho'}$, at which fish enter the exploited phase will be given (remembering that $W_{\rho'}$ is constant) by the equation

$${}_2t_{\rho'} = t_\rho + \frac{1}{K}\log\left(\frac{W_\infty{}^{1/3} - {}_2W_\rho{}^{1/3}}{W_\infty{}^{1/3} - W_{\rho'}{}^{1/3}}\right)$$

so that in this case the duration of the pre-exploited phase has changed. As before the quantity $(t_{\rho'} - t_0)$ is unchanged, but although the number recruited to the population each year has not changed, the number entering the exploited phase is now

$$R'_2 = Re^{-M({}_2t_{\rho'} - t_\rho)}$$

where M refers to the natural mortality coefficient in the post-recruit phase. Again ignoring any small change in the duration of the fishable life-span we have

$$\frac{{}_2Y_W}{{}_1Y_W} = e^{-M({}_2t_{\rho'} - {}_1t_{\rho'})} \quad \ldots \quad \ldots \quad \ldots \quad (9.10)$$

If a change in the pre-recruit growth rate involves a change both in the age and in the weight at recruitment, it may be analysed by a combination of the above methods.

The above analysis shows that whether the effect of a change in the pre-recruit growth results in a change in either the age or the weight at which fish migrate to the exploited area, the only appreciable effect on the exploited phase of the population, and hence on the yield, comes from a change in the number of fish entering the exploited phase each year. This is so despite the fact that in both cases there is a change in the weight-at-age of fish in the exploited phase. Equations (9.9) and (9.10) provide a direct means of assessing the effects of a given change in pre-recruit growth on the steady yield from the exploited phase and thus can be used to investigate problems such as whether deliberate 'thinning' of the pre-recruit phase would increase the yield from the adult stock. In practice, it would be necessary to know the pre-recruit growth rate in order to arrive at an approximate estimate of ${}_2t_{\rho'}$ and also, if recruitment to the exploited area takes place at a threshold *weight*, the natural mortality towards the end of the pre-recruit phase. If it is not known whether recruitment is a function of weight or age or both, it is still possible to calculate two estimates of ${}_2Y_W$ between which the true value will lie.

9.2.2 *Changes in growth pattern during the exploited phase*

The consequences of a discontinuity in the growth rate occurring during the exploited phase are rather different. If the discontinuity is not marked, it may be sufficient to fit a single growth equation to the whole range of data, thereby achieving an effective smoothing of the latter. Sometimes, however, it may be necessary to fit an equation to each phase of growth. For example, if there is a marked change in growth at the onset of maturity at age t_η, where $t_\eta > t_{\rho'}$, there would be two distinct patterns of growth in the exploited phase. In this case it would be possible to obtain values ${}_1W_\infty$, ${}_1K$ and ${}_1t_0$ for the premature phase, and ${}_2W_\infty$, ${}_2K$ and ${}_2t_0$, for the mature phase. The yield from the population is then given by

$$Y_W = FR'\left\{{}_1W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-n_1K(t_{\rho'} - {}_1t_0)}}{F + M + n_1K}\left(1 - e^{-(F+M+n_1K)(t_\eta - t_{\rho'})}\right)\right.$$

$$\left. + {}_2W_\infty e^{-(F+M)(t_\eta - t_{\rho'})} \sum_{n-0}^{3} \frac{\Omega_n e^{-n_2K(t_\eta - {}_2t_0)}}{F + M + n_2K}\left(1 - e^{-(F+M+n_2K)(t_\lambda - t_\eta)}\right)\right\} \quad .. \ (9.11)$$

9.3 Weight Differences between Individuals of the Same Age

In the other parts of §9 the method of representing growth implies that all fish of a given age are the same weight, and although this is never so in practice we have suggested, when first introducing the problem in 3.4, that it will be sufficient for most purposes to refer to the mean weight of fish at each age. In this section we consider certain of the situations for which this simplification may not be satisfactory. It is possible, for example, that the variation in growth rate among individuals of a given year-class would need to be taken into account when developing more exact relationships between growth and population density than we shall attempt in §9.4.3. Thus, intra-specific competition for food might be expected to result in the establishment of a hierarchy, with those individuals possessing the greatest intrinsic growth ability being able to obtain food at the expense of the rest of the population. On the other hand, it may be that differences arising from differing intrinsic metabolic rates will be negated by a tendency for those individuals that are physiologically more active than the average to succumb sooner under adverse conditions (Allee, 1951, p. 103); that is, the magnitudes of K and M may be correlated. We do not attempt to discuss problems of this kind in the present paper, * except in the special case of competition and growth differences between the two sexes of a population (§11.2.1). There is one phenomenon, however, which originates from the variation in growth rate among individuals of a given brood, of which some appreciation can be made by the methods already developed, namely the simultaneous entry of several age-groups of fish into the exploited area, or their simultaneous appearance in the catch.

Data given in §15.1.3 for the North Sea plaice shows that several age-groups enter the exploited phase during a period of about three months. We suggest that an explanation of this phenomenon could be based on the following three postulates:—

(i) That there is variation in the growth rate among individuals comprising each year-brood during the phase of the life-history prior to entry to the catch.

(ii) That actual growth is restricted to a limited season each year, approximately corresponding to the period during which entry occurs.

(iii) That the entry of fish to the catch occurs only by virtue of their reaching a certain threshold weight.

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*Von Bertalanffy's (1950b) derivation of the allometric growth equation from general considerations of competition between parts of a system suggests a possible line of approach.

In the case of the North Sea plaice fishery, criteria (i) and (ii) are satisfied but the gear does not itself determine a threshold weight for entry to the catch, since the mesh at present in use is small enough to retain most of the fish found on the main fishing grounds. When analysis of the catch is based upon market samples, however, an apparent threshold weight for entry to the catch is found, which may be partly due to the operation of a minimum legal size limit for the species. In other cases it might be caused by the selective properties of the gear in use, or there might be a natural threshold weight for recruitment to the exploited area in addition to a further threshold imposed subsequently by the above 'artificial' means. The concept of a threshold weight for recruitment to the area does not necessarily imply that fish suddenly migrate when they reach a threshold size, although this may happen if the recruitment migration should be caused by the onset of maturity, i.e. if it is the first spawning migration.* We show in §15.1.2 that the movement of plaice from the nursery grounds on the Dutch, Danish and German coasts to the main exploited area is a continuous process and more in the nature of a 'diffusion' than a directional migration. Because there is also a tendency for the larger members of each year-class to be found further away from the coast than the smaller ones, the consequence is that recruits of all age-groups tend to be of a similar size. Since the segregation of members of a year-class into several 'sub-groups' occurs at the first weight-threshold reached during life, we base the following analysis on the general case of the weight-threshold being that for migration to the exploited area. The adaptations of these methods required when there is only an artificial weight-threshold are slight and will be readily seen.

We may expect variations in growth rate to be due partly to intrinsic metabolic differences between individuals and partly to differences in their consumption of food as a result of non-uniform distribution of the latter.† In §9.4.1 the physiological significance to be attached to the growth parameters K and W_∞ of the von Bertalanffy equation is discussed, and anticipating this we here represent a variation in growth rate among individuals of a given brood by appropriate variations in both parameters.

Let us suppose that a proportion of the fish comprising a given year-class possess a certain range of combinations of values of K and W_∞ that result in these fish having a faster growth during the pre-recruit phase than the remainder of the year-class, and which enables them to reach the threshold weight for recruitment during a certain growth season. This sub-group will therefore migrate to the exploited area during the course of that season, and we shall call their number ${}_1R$. Similarly, a further number, ${}_2R$, will possess a range of values of K and W_∞ that result in their growth being slower, but sufficiently fast to reach the threshold weight during the growth season of the following year; and so on for all subsequent growth seasons until the whole year-class has entered the exploited area. For example, if variations in K alone were responsible for the differences in growth rate, and these were established on hatching from the egg and were distributed normally in the brood, we should have

$${}_1R = \frac{{}_1cE}{\sigma\sqrt{2\pi}}\int_{{}_1K}^{+\infty} e^{-(K-\bar{K})^2/2\sigma}dK\;;\quad {}_2R = \frac{{}_2cE}{\sigma\sqrt{2\pi}}\int_{{}_2K}^{{}_1K} e^{-(K-\bar{K})^2/2\sigma}dK\;;\quad \text{etc.}$$

where $\bar{K}$ is the mean value of K for the whole brood, E is the total number of eggs laid, and ${}_1c$, ${}_2c$, etc. are factors defining the survival of ${}_1R$, ${}_2R$, etc., recruits from the corresponding fractions of the total egg-production. In practice, the values of ${}_1R$, ${}_2R$, etc., would be obtained from age-composition data (see §15.1.3). Again, we need be concerned only with the growth of each sub-group after it has entered the exploited area, since if this is known, the yield from the whole year-class, and hence the annual yield from the population in a steady state, is obtained by summing the yields from all sub-groups.

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*Investigation of factors influencing the migration of animals have shown that in a number of instances a certain physiological condition—associated with a minimum size—must be attained before migration takes place. Examples among fish are the British salmon (*Salmo salar*), the evidence being summarised by Allen (1944), and the eel (*Anguilla anguilla*) (Frost, 1945).

†It is relevant to mention here that Rodd (1946) has stated that although salmon and trout fry hatched from large eggs are bigger than those from small eggs, this factor does not in any appreciable way affect the size of the adults.

We shall define by ${}_rK$ and ${}_rW_\infty$ the parameters describing the post-recruit growth of any sub-group ${}_rR$, recruited at age ${}_rt_\rho$. These individuals will not necessarily all be exactly the same weight on entering the exploited area, but it will be sufficient for the present purposes to assume they are, and to define this weight as the threshold weight for recruitment, denoted by W_ρ. The post-recruit growth of the rth sub-group is then defined by the equation

$${}_rw_t = {}_rW_\infty \left(1 - e^{-{}_rK(t - {}_rt_0)}\right)^3$$

where

$${}_rt_0 = {}_rt_\rho + \frac{1}{{}_rK} \log \left\{1 - \left(\frac{W_\rho}{{}_rW_\infty}\right)^{1/3}\right\}$$

(cf. (9.6))

Depending on the selective properties of the gear, fish will first become liable to capture when they reach another threshold size $W_{\rho'}$ (the mean selection weight), though the corresponding age will differ for each sub-group. For the sub-group ${}_rR$ we can put

$${}_rW_\infty\left(1 - e^{-{}_rK({}_rt_{\rho'} - {}_rt_0)}\right)^3 = W_{\rho'} = \text{constant}$$

thus defining ${}_rt_{\rho'}$. Putting also

$${}_rt_{\rho'} - {}_rt_\rho = {}_r\rho$$

$$\text{and} \quad t_\lambda - {}_rt_{\rho'} = {}_r\lambda$$

the yield from the sub-group ${}_rR$ is

$${}_rY_W = F_r R_r W_{\infty} e^{-M_r\rho} \sum_{n=0}^{3} \frac{\Omega_n e^{-n_rK({}_rt_{\rho'} - {}_rt_0)}}{F + M + n_rK} \left(1 - e^{-(F + M + n_rK)_r\lambda}\right) \quad .. \quad (9.12)$$

The yield from all the Φ sub-groups which comprise the whole year-class R is

$$Y_W = \sum_{r=1}^{\Phi} {}_rY_W \quad .. \quad .. \quad .. \quad .. \quad (9.13)$$

which is also the annual yield from the population. It will be seen that by these methods we can take account of the fact that the faster growing members of a year-class will be depleted by fishing to a greater extent than the slower growing individuals, and that the size composition of a fully recruited year-class will differ from that obtaining before the initiation of recruitment. The relationship between the total recruit numbers and the population density when there is recruitment into several age-groups, has been mentioned in §6.1.4.

9.4 DEPENDENCE OF GROWTH ON POPULATION DENSITY

9.4.1 *Some preliminary concepts*

The variation of growth with density in fish populations is perhaps the best established of the density dependent effects which we consider in this paper, and a review of the subject has been published by Hile (1936). Since then a number of other instances have been recorded: indeed, as investigations of the effects of density changes in fish populations have developed, it has become rare to find a case in which changes in growth have not occurred, the most outstanding example known to us being that of the perch (*Perca fluviatilis* L.) in Lake Windermere, whose growth has remained constant despite a ten-fold change in density (LeCren, 1949). The reason for its frequent observation is primarily that growth depends critically on the food supply, which, in turn, is closely dependent on the population density; because of the plasticity of growth in adult fish it would therefore be expected that the response of a fish population to changes in density would be primarily a change in growth rate. If the variations in density are large and the food supply limited, the effect on growth may easily outweigh that of all other factors, such as variations in temperature, and be readily detected from data. It may be that factors other than the food supply cause growth to be affected by density; thus Willer (1929) has shown that dense crowding under experimental conditions can cause a retardation of growth even though there is sufficient food. Such a phenomenon has seldom, if ever, been demonstrated in nature, and in this section we shall take it that changes in growth with population density are due to corresponding changes in the food supply.

There are two approaches to this problem. If sufficient data are available an empirical expression can be fitted relating growth to population density, and incorporated into hypothetical population models (§9.4.2). The other method is to undertake an analysis of the interaction between the fish population and its food supply, introducing the concept of grazing and the dynamics of the populations of the food organisms (§9.4.3). Clearly, the one adopted in a particular case must depend on the type of data available, but only the analytical method, forming the basis of a study of the populations of the area as a community, can lead to a full understanding of the factors underlying the observed events (see §1). Nevertheless, the relationship between the growth pattern of individuals comprising a natural population (as opposed to the growth increment over a short period) and factors such as the density and size-distribution of the population, its grazing activity on food supplies of varying abundance and the dynamics of the food organisms, has received relatively little attention in the past from students of population dynamics, though some knowledge of it is vital to the practical understanding of a predator-prey system. Hence the synthesis we offer in §9.4.3, must be regarded as tentative in that there are few data or established methods that could be used as a guide to its formulation.

Whichever approach is adopted, there are certain questions common to both which require discussion; one of these is the way in which a change of growth rate resulting from a change in population density is to be represented, and for this purpose we shall assume that a change in growth rate from such a cause is due solely to a change in the amount of food consumed by a fish. When discussing the derivation of the von Bertalanffy equation, it was mentioned that only two primary coefficients need to be specified, i.e. those referring to the rates of anabolism and catabolism. The process of catabolism is the breakdown of existing body materials, and we should expect the rate of catabolism to be affected only by the amount of body material to be broken down, i.e. the weight of the organism, and the general level of metabolic activity. The rate of anabolism, on the other hand, while dependent on the metabolic activity and dimensions of the organism, must also be affected by the rate at which nutrient materials are brought into contact with the absorbing surfaces; in other words, by the rate of consumption of food by the organism. It is possible that different levels of food consumption may result in some change in the general metabolic activity, and thus affect the rate of catabolism as well as that of anabolism, but these changes are likely to be of minor importance compared with the variations in the rate of anabolism that would result directly from the considerable changes in rate of food consumption with which we shall be concerned. From this it would seem that changes in growth resulting from changes in population density are most suitably represented by appropriate changes in the magnitude of the coefficient of anabolism. Now the coefficients of anabolism and catabolism, E and k, do not appear as such in the growth equation, though we have the relationships

$$W_\infty = q\left(\frac{3E}{k}\right)^3; \quad K = \frac{k}{3}$$

We shall therefore regard K as independent of changes in food consumption, and represent changes in growth rate by appropriate variations in the magnitude of the parameter W_∞.*

Direct supporting evidence of this comes from certain experimental work carried out by von Bertalanffy (1934).† By using the rate of nitrogen excretion and the rate of loss of weight in starving animals (certain crustacea, molluscs and fish), von Bertalanffy was able to obtain estimates of the catabolic coefficient K that agreed well with those obtained by fitting the equation to weight-at-age data of the same animals *under conditions of normal growth.* This would suggest that the value of the parameter K does not vary greatly even over a wide range of food consumption. Experiments conducted by Yoshihara (1952) on the growth of carp, in which he supplied the same amount of food to ponds stocked with various densities of fish, are also relevant here. Although they were continued over two seasons only, the results indicate that the growth differences were, within the limits of accuracy of the data, due entirely to differences in the upper limits of size to which the fish were tending. In terms of the von Bertalanffy equation this means that it was the parameter W_∞, and not K, that was affected by variations in the food consumption.

We have not been able, for this paper, to undertake an analysis of the available growth data for the plaice and haddock, or other North Sea demersal species, with a view to putting these ideas to the test, and it is possible that controlled experiments would be required to eliminate the effects of factors other than food consumption which influence the rate of growth under natural conditions. It may be noted, however, that the methods to be described are not necessarily invalidated if it should be found that changes in K occur which cannot be neglected. In this case we might obtain, from data, the variation of K with W_∞ for various levels of food consumption, and express K in terms of W_∞ by an appropriate simple function. From the theoretical point of view, this would mean that we would still have to deal with one independent parameter only, i.e. W_∞, in attempting to predict the growth rate in given circumstances.

Another problem that requires attention at this stage concerns the range of population density and consequent growth rate within which the population models of this section can be regarded as valid. Evidence on this would seem to be quite definite; it is that when once fish have passed beyond the larval or juvenile phases their growth is remarkably plastic and can vary within wide limits without harming them. For example, fish in temperate regions regularly cease feeding altogether in the winter months; moreover, fish can be kept healthy under experimental conditions for long periods when supplied with bare maintenance rations—even during what would normally be the growing season. Evidence of this kind in the case of plaice (Dawes; 1930, 1931) is presented and analysed in detail in §16.4.2, and shows that by adjustment of the food supply, the rate of growth can readily be varied, without ill-effect, between zero and a figure many times greater than that found in the North Sea population. The great plasticity of growth of plaice is, of course, the basis of the many transplantation experiments that have been carried out with this species, the increase of growth when fish are moved to areas having a more abundant food supply more than offsetting, in favourable circumstances, the cost of transportation and losses in transit (Tåning, 1952). Perhaps the most striking evidence in natural conditions comes from the work on the stunted growth of fish in dense populations living in confined areas such as small lakes. The extremely slow growth that can result in these circumstances has been studied in detail by Alm (1946) in connection with the perch (*Perca fluviatilis* L.) of certain Swedish lakes. Alm investigated lakes in which the growth of perch virtually ceased after the first year or so, although there was only a slight indication that the natural mortality rate was higher than in lakes containing normally growing fish. He concluded that the physical environment of the various lakes was to some extent responsible for the differences in growth, and did not exclude the possibility of there being genetic differences in growth capacity, but by far the most important factor was the supply of food. The author tested this by transplantation, and by decreasing the population density by fishing and introducing predators; normal growth could be restored by either means, showing that the effects of variations in food consumption were completely and rapidly reversible. Cases of stunted growth in perch populations in Dutch lakes have been studied by Deelder (1951), whose findings agree closely with those of Alm. Deelder showed that the stunted perch stopped growing after having reached a length of about 13 cm., although they could live for several years after, and that the cessation of growth was due to a shortage of the small fish that formed the food of perch of this size and greater. As a consequence, the majority of the stunted fish failed even to reach the minimum legal size of 18 cm.—a situation exactly parallel to that predicted by the population models developed in this section (see §18.4.1). Finally, mention should be made of methods used in commercial fish culture in China, described by Lin (1940). One of these is to adjust the supply of food so that the fish (certain species of carp) are kept for as long as required at the most economical size, which may be much less than the maximum they can attain.

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*Allen (1941b) found that the condition factor, w/l^3, of salmon in different rivers and at different seasons, varies directly with the growth rate; but in such a case, where growth is not truly isometric, the effect needs to be expressed by appropriate variations of W_∞ with K constant. The existence of this 'fattening', however, makes it clear that it is preferable to use weight-growth curves obtained by direct measurement, rather than converted length-growth curves, in exploitation equations (see Parts III and IV).

†It should be mentioned that von Bertalanffy does not discuss specifically, in the publications mentioned in §3.3, this problem of the relation between the parameters of anabolism and catabolism and the rate of food consumption.

In the light of the above evidence it therefore seems reasonable to suppose that we may allow the growth rate—as predicted by a population model— to fall virtually to zero before needing to introduce compensating factors, such as an increase in the natural mortality rate. In effect, this means that we can allow the value of W_∞ to decrease until it reaches W_p, the weight at which fish enter the exploited area, when the food eaten per fish will be just sufficient to satisfy maintenance requirements alone. The upper limit of growth rate that can be permitted involves no particular complications and corresponds to the growth rate of fish that are obtaining the maximum amount of food they can eat. This *limiting growth rate*—defined by the parameter $W_{\infty L}$ — has to be determined by experiment, and we discuss the problem in more detail in §9.4.3.2.2.

9.4.2 *Empirical relationships between growth and population density*

We need not discuss this method in great detail here, since the main problems concern the analysis of data, and are examined with examples in §16.4.1. The essential requirement is a series of simultaneous observations of growth rate and population density, and these may come either from several equilibrium levels of population abundance, or from a series of year-to-year fluctuations. In the former case there would be a full series of weight-at-age data at each level, and the value of W_∞ could be determined in the usual way (see §16.2). In the latter, it would be necessary to determine a value of W_∞ for each year, from the modified form of the von Bertalanffy equation

$$_xW_\infty = \left[\frac{{}_xw_{t+1}^{1/3} - {}_xw_t^{1/3}\,e^{-K}}{1 - e^{-K}}\right]^3 \quad \ldots\ \ldots\ \ldots \quad (9.14)$$

where w_t and w_{t+1} are the weights of individuals of any year-brood at age t and $t+1$ respectively, at the beginning and end of the year X. In either event, the series of values of W_∞ could be plotted against the corresponding estimates of the annual mean population density, and the data fitted by the simplest expression which was adequate for the purpose.* For example, W_∞ might be found to be linearly related to the annual mean population biomass, in which case we could write

$$W_\infty = a + b\bar{P}_W \quad \ldots\ \ldots\ \ldots\ \ldots \quad (9.15)$$

where a and b are constants obtained by finding the regression of W_∞ on $\bar{P}_W$. We also have $\bar{P}_W$ given in terms of W_∞ from (5.8), viz.

$$\bar{P}_W = RW_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_\rho - t_0)} \left\{ \frac{1 - e^{-(M+nK)\rho}}{M + nK} + \frac{e^{-(M+nK)\rho}\left(1 - e^{-(F+M+nK)\lambda}\right)}{F + M + nK} \right\}.$$

and also

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*The special problems arising when fluctuating data are utilised in this way are discussed further in §16.4.1.2.

$$t_{\rho'} = t_\rho + \frac{1}{K} \log \left\{ \frac{W_\infty{}^{1/3} - W_\rho{}^{1/3}}{W_\infty{}^{1/3} - W_{\rho'}{}^{1/3}} \right\}$$

The required value of W_∞ for given values of F and $W_{\rho'}$—that is, fishing intensity and gear selectivity—is that which satisfies all three equations above. These equations can also be used to investigate effects on the growth rate of a permanent change in the magnitude of R, for which it is only necessary to know the relative, and not the absolute values of R. With W_∞ thus determined, the value of any desired population characteristic, such as the annual yield, can be assessed by means of the equations given in §§4 and 5.

These methods may readily be extended to deal with certain complications that are to be expected in practice. For example, whether we are dealing with changes in growth of the post-recruit phase only—in which case the weight and age at recruitment will be constants—or of both the pre- and post-recruit phases, a discontinuity in growth will occur at age t_ρ. This will mean that a value of t_0 has to be determined for each value of W_∞, as discussed in §9.2.1.

Another complication that may arise is that the type of food consumed by the population may not be the same for fish of all ages. In this case we should expect to find that the growth of certain age-groups, or certain bands of age-groups, varied only with their own abundance and not with that of the whole population, the degree of variation differing according to the relative abundance of the various types of food organisms involved. This situation might be dealt with by dividing the population into phases—each phase being homogeneous with respect to the type of food consumed by it—determining values of W_∞ for each phase, and relating these to the corresponding abundance of that phase. The details of the method to be used would depend on whether the change over from one type of food to another was primarily a function of weight or of age, and the discussion of §9.2.1 would be relevant to this problem. With the values of W_∞ for the various phases of the population having been determined for given values of F, $W_{\rho'}$ and R, the yield from the whole population could be evaluated by means of the method described in §9.2.2.

Further, there is the possibility that fishing itself may be a direct cause of some destruction of fish food (Gilson, 1928, Hickling, 1946a). A trawl, for example, probably crushes a proportion of the benthic animals which cannot move from its path or burrow in the sand, and it is a common occurrence for certain species of the bottom fauna to be brought up in a trawl. These, however, do not usually include the most important food species such as worms and molluscs, nor do we know of any direct evidence to show that their destruction represents an appreciable part of the total mortality of food organisms*. A theoretical treatment of the problem involves a consideration of the dynamics of the food populations, and is therefore given later in §9.4.3.4, but we may mention here certain implications of the destruction of fish food by the fishing gear on the use of empirically determined relationships between growth and density.

In so far as the effect exists, it will automatically be taken into account in any relationship between growth and density obtained from data in which density changes are due to differences in the fishing effort. A population model containing such a relationship will therefore give correct assessments of the effects of proposed changes in fishing mortality, assuming the latter are to be brought about by changes in the amount of trawling. If the model is to be used to predict the effects of changes in mesh size, then we should expect to find that the growth-density relationship contained therein is underestimated, since it is not likely that the particular mesh size has much influence on the extent of the destruction of bottom fauna by trawls. The converse is true for growth-density relationships determined from data in which natural fluctuations in year-class abundance are responsible for the changes in population density. The resulting population models are likely to give correct assessments of the effects of changes in mesh size but not in the amount of trawling, since if there is any destruction of fish food by trawling it will tend to counteract the effect of changes in population density on the abundance of food and hence growth rate.

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*Experimental evidence in support of this statement for the food of North Sea plaice is given in a recent paper by Graham (1955).

9.4.3 *The relationship between growth and food consumption and their dependence on population density*

The general procedure we are following in this paper is to treat the fish population as the prey and the fishing fleet as the predator; in the present section we extend this to the next level of the food-chain or Eltonian pyramid (Elton, 1927), and regard the fish population, in turn, as predator, and its food as the prey. There is one important difference between these two predator-prey systems which has a considerable influence on their theoretical treatment. The yield obtained by a given fishing effort can be of any size depending primarily on the abundance of the fish, though in practice the latter exerts an indirect limitation on the magnitude of the fishing effort through factors (primarily economic) external to the system. On the other hand, if we have a fish population of a given size and age-composition containing individuals growing at a known rate, the amount of food of a given nutritional value being consumed annually by the population—which is analogous to the yield obtained by man from the fish population—is precisely defined. The first requirement, of which there is no exact counterpart in the man-fish interaction, is therefore to develop a theoretical model giving the amount of food consumed annually by a fish population for which these characteristics are specified. We do this in §9.4.3.1 and then use it to investigate the relationship, qualitative aspects of which have been discused by LeCren (1949), between the annual food consumption, the availability of the food and the density of the fish population and its resultant growth (§9.4.3.2). Since the characteristics of the fish population depend in part on the fishing mortality to which it is exposed, the resulting models cover three levels of the food-chain and can be used to predict the yield corresponding to various fishing intensities or mesh sizes in the same way as we have discussed in §9.4.2. To conclude §9.4.3 we give a short note on the effects of aggregation of the food population on the efficiency of its utilization by fish (§9.4.3.3), and on the case in which the fishing gear is responsible for some destruction of the food organisms (§9.4.3.4).

Throughout §9.4.3 we shall be concerned only with changes in growth of the post-recruit phase of the population, and shall assume that a change in the abundance of that phase has a uniform effect on the growth rate of all fish in it, i.e. can be described by a value of W_∞ which is valid for fish of all ages between t_ρ and t_λ. As a partial corollary to this we shall assume, except in §§9.4.3.2.4 and 9.4.3.2.5, that the food consumed is either homogeneous with respect to nutritional value or, if heterogeneous, has a mean nutritional value which remains constant. Where the growth pattern cannot be described by a single value of W_∞, it may be that the food consumed by fish of different sizes is not the same. In this case either of the methods to be described can be modified in the way suggested in the previous section, or it may be necessary to treat the population as heterogenous in the sense used in §11.2.

9.4.3.1 *Evaluation of the total annual food consumption, Ξ*

9.4.3.1.1 *Efficiency of food utilisation constant*

The total amount of food consumed by a year-class of fish during its post-recruit phase, i.e. while in the exploited area, can be regarded as consisting of two portions, one being used to satisfy maintenance requirements and the other for growth purposes. In accordance with general physiological evidence we shall take it that the rate of consumption of maintenance food by a fish, $d\xi_m/dt$, will be a function of its weight, and we may put

$$\frac{d\xi_m}{dt} = \zeta w^{\jmath} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (9.16)$$

where ζ is the maintenance food coefficient, which for the moment we shall regard as constant. There seems to be little detailed evidence concerning the maintenance metabolism of fish, though an analysis of the data of Dawes (1931) on the maintenance food requirements of plaice given in §16.4.1, gives an estimate of the value of j of almost exactly 2/3. This value is not inconsistent with Brown's (1946) data for the brown trout (though Pentelow (1939) concluded that the maintenance ration for this species, as well as varying greatly with temperature, increased roughly in proportion to the weight of the fish), nor with the general evidence relating to the maintenance requirements of mammals. Thus Brody (1945), summarising what is known about mammals, concludes that basal metabolism varies approximately with surface area, the power of the body weight being about 0.7. While less is known concerning maintenance metabolism, Brody considers that it varies with body weight in the same way as basal metabolism.

For the following treatment we shall therefore deal with the case in which j has the value 2/3, so that the rate of consumption of maintenance food by the total number of fish which survive to age t is given by

$$\frac{d\Xi_m}{dt} = \zeta w_t^{2/3} N_t$$

Hence the total amount of food consumed for maintenance by the year-class throughout its post-recruit life, which is the same as the annual amount of food consumed for maintenance by the population in a steady state (cf. §4), is given by

$$\Xi_m = \zeta \int_{t_\rho}^{t_\lambda} w_t^{2/3} \, . \, N_t \, . \, dt$$

which, on integration, becomes

$$\Xi_m = \zeta R W_\infty^{2/3} \sum_{n=0}^{3} \Omega'_n e^{-nK(t_\rho - t_0)} \left\{ \frac{1 - e^{-(M+nK)\rho}}{M+nK} + \frac{e^{-(M+nK)\rho}\left(1 - e^{-(F+M+nK)\lambda}\right)}{F+M+nK} \right\} \qquad (9.17)$$

where

$$\Omega'_0 = 1$$

$$\Omega'_1 = -2$$

$$\Omega'_2 = 1$$

$$\Omega'_3 = 0$$

It will be noted that (9.17) is similar in many respects to (5.8) for the annual mean biomass, and a convenient way of writing (9.17) is

$$\Xi_m = \zeta \bar{P}_{W^{2/3}} \quad .. \quad .. \quad .. \quad .. \qquad (9.18)$$

If j were found to have a value differing appreciably from 2/3, and was not a multiple of 1/3, we should not integrate directly but put j successively equal to multiples of 1/3 and solve for Ξ_A by interpolation.

Dealing now with the fraction of the food consumed that is utilised for growth, we first need to determine the total growth increment produced by the population each year, which we shall call the *annual production*, A.P.*

If we denote by $(dw/dt)_t$ the rate of growth of an individual at age t, the total amount of growth produced by a year-class throughout its post-recruit life, which for a population in a steady state is the same as the annual production, can be written as

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*We are using the term 'production' in the sense of Tansley (1929) and 'corrected production' of Lindemann (1942), and it is also equivalent to the integrated form of the 'gross production rate' of Clarke (1946) and Ricker (1946). We would refer the reader to Krumholtz (1948) and Macfadyen (1948) for a review of the definitions of the terms 'production', 'productivity' and 'yield' that have appeared in the literature.

$$A\,.\,P\,. = \int_{t_\rho}^{t_\lambda} \left(\frac{dw}{dt}\right)_t . N_t dt \qquad \ldots \quad \ldots \quad \ldots \qquad (9.19)$$

This is analogous to the basic equation postulated by Allen (1950), who uses either an exponential growth equation or that of Brody (1945) (see §9.1). With the von Bertalanffy equation our usual procedure would be to write

$$w_t = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)}$$

from which

$$\left(\frac{dw}{dt}\right)_t = W_\infty \sum_{n=0}^{3} - nK\Omega_n e^{-nK(t-t_0)}$$

Substituting in (9.19) and integrating gives

$$A\,.\,P\,. = RW_\infty \sum_{n=0}^{3} - nK\Omega_n e^{-nK(t_\rho - t_0)} \left\{ \frac{1 - e^{-(M+nK)\rho}}{M+nK} + \frac{e^{-(M+nK)\rho}\left(1 - e^{-(F+M+nK)\lambda}\right)}{F+M+nK} \right\} \qquad (9.20)$$

But we later need to express the rate of growth in a form that does not contain t explicitly, and to this end we return to the original differential form of the von Bertalanffy equation given in §3.4, i.e.

$$\frac{dw}{dt} = Hs - kw$$

Substituting for H, s and k from the relationships set out in that section, viz.:

$$H = \frac{3q^{2/3}KW_\infty{}^{1/3}}{p}$$

$$s = \frac{pw^{2/3}}{q^{2/3}}$$

$$k = 3K$$

we obtain

$$\frac{dw}{dt} = 3K\left(W_\infty{}^{1/3}\,w^{2/3} - w\right) \qquad \ldots \quad \ldots \quad \ldots \qquad (9.21)$$

for the rate of growth of a fish of weight w. For a given value of W_∞ we may express w in terms of t as before, and write (9.19) in the form

$$A\,.\,P\,. = 3K\int_{t_\rho}^{t_\lambda} (W_\infty{}^{1/3}\,w_t{}^{1/3} - w_t)N_t\,.\,dt \qquad \ldots \quad \ldots \qquad (9.22)$$

Since

$$\int_{t_\rho}^{t_\lambda} w_t{}^{2/3}\,.\,N_t\,.\,dt = \bar{P}_{W^{2/3}} \quad \ldots \quad \ldots \quad \ldots \qquad \text{(see (9.18))}$$

and

$$\int_{t_\rho}^{t_\lambda} w_t\,.\,N_t\,.\,dt = \bar{P}_W{}^{2/3}$$

(9.22) becomes

$$A\,.\,P\,. = 3K(W_\infty{}^{1/3}\,\bar{P}_{W^{2/3}} - \bar{P}_W) \quad .. \quad .. \quad .. \quad (9.23)$$

which will be found to be identical with (9.20).

Now, the food consumption required to produce this *A* . *P* . may be represented as

$$\Xi_g = \frac{A\,.\,P\,.}{\varepsilon} = \frac{3K}{\varepsilon}\left(W_\infty{}^{1/3}\,\bar{P}_{W^{2/3}} - \bar{P}_W\right) \quad .. \quad .. \quad (9.24)$$

where ε is the *efficiency of utilization of food for growth*. For a given type of food, ε is the ratio of a given increment of weight to the amount of that food required to produce it, and for the moment we shall assume (as in the case of the maintenance food coefficient ζ) that it is a constant. We are here using the term 'efficiency of utilisation' to refer purely to the sum of the physiological processes involved in the absorption of food and its conversion to body substance, which is in accordance with physiological practice (e.g. Brody, 1945). It has nothing to do with the efficiency with which fish graze the food populations (Ricker, 1946; Allen, 1951), a phenomenon which might perhaps be more appropriately called the 'efficiency of predation'. It differs also from the definition adopted by LeCren (1949), which is, in effect, the fraction of the total food consumed that is available for growth as opposed to maintenance requirements. Thus the 'efficiency of utilisation' according to LeCren is zero when the whole of the food consumed is needed for maintenance, though it is in these circumstances that the true physiological utilisation of food is at nearly maximum efficiency (see §9.4.3.1.2).

The total amount of food consumed annually by a steady population, for both maintenance and growth, can now be obtained by summing (9.18) and (9.24), giving

$$\Xi = \Xi_m + \Xi_g = \left(\zeta + \frac{3KW_\infty{}^{1/3}}{\varepsilon}\right)\bar{P}_{W^{2/3}} - \frac{3K}{\varepsilon}\bar{P}_W \quad .. \quad .. \quad (9.25)$$

9.4.3.1.2 *Efficiency of utilisation varying with the amount of food consumed*

We may extend the above methods to an analysis of the case in which the maintenance coefficient, ζ, and the efficiency of utilization of food for growth, ε, are not constants. While it does not seem that the variation of either with size of the individual is likely to be important, there is evidence for many animals to indicate that the efficiency of utilisation of food energy decreases as the amount of food consumed increases. Thus Brody (ibid) gives much data for higher vertebrates which support this statement, while the work cited above of Dawes on plaice, and Brown with trout, confirms it for these species (see §16.4.2.3). The phenomenon was also found by Ricker (1949b) in bluegills (*Lepomis macrochirus*) and by Moore (1941) in several species of American freshwater fish.

Brody and Procter (1933) and Kostitzin (1939, p. 180) have discussed the variation of efficiency of utilisation of food energy with the amount of food consumed, and have deduced theoretical relationships between the net energy x assimilated by an organism from a given amount of gross food energy X. That due to Kostitzin would seem to be of more general significance, and using his terminology the expression is

$$x = \frac{1}{k}\tanh(k\sigma X) \quad .. \quad .. \quad .. \quad (9.26)$$

where k and σ are constants, the latter being the value of the maximum efficiency of utilization of food energy, i.e. the limit to which the efficiency tends as the food consumption falls to zero. In accordance with the general requirements of the data, the change of x with X given by this expression follows a curve which is concave downwards and which approaches a finite asymptote as X → ∞. If we put $X = \infty$ in the equation above, we obtain $x = 1/k$, so that $1/k$ is seen to be the maximum possible value of the net assimilated energy.

We now need to adapt Kostitzin's equation to a form suitable for incorporation into the expressions of §9.4.3.1.1, and which is compatible with the limited data available on the physiology of growth in fish. In the first place, the quantities X and x refer to discrete amounts of gross alimentary energy and net assimilated energy respectively, but in a general sense we may identify them with the total amounts of gross energy and net energy obtained by a fish during the course of a year. This interpretation is exact if the total amount of food consumed by a fish during the course of a year can be regarded as composed of a large number of small discrete amounts of equal size, each of which is digested before the next is taken in, and if changes in the annual food consumption result from equal changes in each of these amounts. It is not necessary for feeding to procede at a uniform rate during the year, that is, it is permissible for there to be one or more periods during which no food is consumed. The interpretation is still approximately true if the discrete units of food are not equal, provided they form a pattern in time which is substantially unchanged from year to year, and is the same at all levels of feeding (see also §9.4.3.3). The relationship between gross energy consumption, X, and food consumption, ξ, of a fish, depends upon the nutritional value, ν, of the food in question, defined as the energy content of a unit mass of food. Since we are regarding the food supply as having a constant nutritional value, we may write $X = \nu \xi$, and substituting in (9.26) gives

$$\frac{x}{\nu} = \frac{1}{\nu k} \tanh (k\sigma\nu\xi) \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (9.27)$$

We have previously defined ε as the efficiency of utilisation of food for growth, but it would seem reasonable to expect that the same efficiency would apply to assimilation of net energy for maintenance purposes. Consequently, we may regard σ of (9.26) as equivalent to the maximum value of ε, and shall denote it by ε_0.

The rate of assimilation of net energy for maintenance by a fish of weight w can now be written as

$$x_m = \varepsilon\zeta w^{2/3}$$

but since the amount of food required for maintenance will vary directly with the efficiency with which it is utilised, the product $\varepsilon\zeta$ will have a constant value Q,* independent of the level of feeding, and will be the maintenance energy requirement per unit 'physiological' surface. Denoting the product $\varepsilon\zeta$ by Q gives

$$\frac{x_m}{\nu} = Qw^{2/3}$$

Since gross energy consumption and food consumption are proportional, we can put

$$\frac{x_g}{\nu} = \frac{dw}{dt}$$

and for a fish of weight w whose growth is specified by the parameters K and W_∞, we have, from (9.21)

$$\frac{x_g}{\nu} = 3K(W_\infty{}^{1/3}\, w^{2/3} - w)$$

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*Although the maintenance food coefficient, ζ, can only be observed experimentally if the level of feeding is just sufficient to satisfy maintenance requirements alone, it will increase as the level of feeding increases above the maintenance level owing to the decreased efficiency of utilisation of food energy. Strictly speaking, therefore, we should define the maintenance food coefficient at the maintenance level of feeding as, say, ζ_m, and if we also define the efficiency of utilisation of food energy at that level by ε_m, then we have

$$\varepsilon_m\zeta_m = \varepsilon\zeta = Q$$

where ε and ζ refer to any level of feeding above that required to satisfy maintenance requirements only.

Consequently, we may express the rate of assimilation of net energy by a fish of weight w in the form

$$\frac{x}{v} = \frac{x_m + x_g}{v} = Qw^{2/3} + 3K(W_\infty{}^{1/3}\,w^{2/3} - w) \quad .. \quad (9.28)$$

By the methods of §9.4.3.1.1 we can now express the amount of net energy assimilated per year by a *population* as

$$\frac{(x)_p}{v} = \int_{t_\rho}^{t_\lambda} \Big\{ Qw_t{}^{2/3} + 3K(W_\infty{}^{1/3}\,w_t{}^{2/3} - w_t) \Big\} N_t\,dt$$

It will be seen that the second part of this expression is the $A\,.\,P\,.$ as defined by (9.22), and integrating gives

$$\frac{(x)_p}{v} = (Q + 3KW_\infty{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W \quad .. \quad .. \quad .. \quad (9.29)$$

(cf. 9.25)

The remaining parameter to discuss is k, the reciprocal of which is the maximum possible value of the net assimilated energy x. If we regard the rate of assimilation of net energy for maintenance as independent of the level of feeding, any differences in the rate of assimilation of total net energy among fish of the same weight must appear as differences in their rate of growth. Consequently, denoting by $W_{\infty M}$ the value of the growth parameter W_∞ that describes the growth curve of a fish growing at the maximum possible rate, the maximum rate at which a fish of weight w can assimilate net energy is, by analogy with (9.28),

$$\frac{1}{kv} = Qw^{2/3} + 3K(W_{\infty M}{}^{1/3}\,w^{2/3} - w)$$

The maximum possible amount of net energy which a given *population* can assimilate during a year, is therefore

$$\left(\frac{1}{kv}\right)_p = \int_{t_\rho}^{t_\lambda} \Big\{ Qw_t{}^{2/3} + 3K(W_{\infty M}{}^{1/3}\,w_t{}^{2/3} - w_t) \Big\} N_t\,dt \quad .. \quad .. \quad (9.30)$$

When we come to integrate (9.30) the need for deriving (9.22) for A . P . using an expression for rate of growth that is not an explicit function of t becomes apparent. Thus we could not determine the maximum possible value of the A . P . , (A . P .)$_M$, of a *given* population by integrating the expression

$$(A\,.\,P\,.)_M = \int_{t_\rho}^{t_\lambda} \left(\frac{dw}{dt}\right)_M .\, N_t\,dt$$

in which the maximum possible rate of growth is expressed as

$$\left(\frac{dw}{dt}\right)_M = W_{\infty M} \sum_{n=0}^{3} - nK\Omega_n e^{-nK(t-t_0)}\ .$$

since this would imply that

$$w_t = W_{\infty M} \sum_{n=0}^{3} \Omega_n e^{-nK(t-t_0)}$$

and hence that the fish comprising the population had been growing *throughout life* at the maximum possible rate whereas, in fact, they must have been growing at the observed rate specified by W_∞. For a population with a given size distribution of fish the maximum possible rate of assimilation of net energy must be defined in terms of the maximum possible rate of growth which fish *of those sizes are theoretically capable of exhibiting*. In other words, we require to specify the rate of growth that the population would take on if its food consumption, and hence its rate of intake of gross energy, suddenly became infinite. Thus we find that integration of (9.30) may be accomplished in exactly the same way as that of (9.22), and we have

$$\left(\frac{1}{kv}\right)_p = \left(Q + 3KW_{\infty M}{}^{1/3}\right)\bar{P}_{W^{2/3}} - 3K\bar{P}_W \quad \cdot\cdot \quad \cdot\cdot \quad (9.31)$$

We have now obtained expressions giving the actual and maximum possible rates of net energy assimilation of a population in terms of its age-composition and growth rate. The final step is to substitute for $(x/v)_p$ and $(1/kv)_p$ of (9.29) and (9.31) in the modified form of Kostitzin's equation (9.27), thus eliminating the nutritional factor v and giving the annual food consumption of the population as

$$\Xi = \frac{1}{\varepsilon_0}\left\{(Q + 3KW_{\infty M}{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W\right\}\tanh^{-1}\left\{\frac{(Q + 3KW_\infty{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}{(Q + 3KW_{\infty M}{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}\right\} \quad (9.32)$$

9.4.3.2. *The relation between food consumption Ξ, the availability of food, and the density and growth of the fish population*

In the previous section we developed equations defining the annual food consumption of a fish population in terms of its abundance, age-composition and the growth rate of the individuals comprising it. Since (9.32) takes into account the change in efficiency of utilisation of food energy with amount of food consumed, this equation can be used to investigate the effect on growth of variations in population density. We discuss this procedure in detail below; at this stage the main problem is to find how the annual food consumption is likely to vary with the availability of food, which involves a consideration of the interaction between the fish population and populations of food organisms.

Unfortunately, few of the relevant data are sufficiently comprehensive and detailed to provide a firm basis for the formulation of theoretical methods, largely because of the complexity of the problem and of the difficulty of studying it under experimental conditions except in the case of the simplest predator-prey systems such as those investigated by Gause (1934). In these circumstances the approach we adopt is to put forward several alternative hypotheses using as a guide such information as is available. In §18.4.2 these hypotheses are applied to the North Sea plaice and we show how some discrimination can be made between them. It should be mentioned here that Ricker (1946) has published a valuable review of the literature on this subject, though a number of the references are to Russian papers, some of which, unfortunately, we have not seen.

9.4.3.2.1 *Hypotheses* (a) *and* (c)

When formulating the simple population models of Part I we assumed that the weight and growth rate of an individual fish at a given age were constant, and in particular, independent of the population density. This assumption, which we shall refer to as *hypothesis* (a), has definite implications as far as the relationship between food consumption and food availability is concerned. Thus one requirement is that the availability of food to any member of the population must be independent of the annual food consumption of the population, and hence in this respect the food supply must be regarded as unlimited; in other words there can be no competition for food between individual fish no matter how great the population density may be. On the other hand, unless the existing growth rate were that which would be found if fish were supplied with as much food as they could eat (which, in general, is not likely to be the case), we must presume that the local density of food on the sea-bed is not so great that fish, during the course of their normal feeding 'sorties', can obtain their 'maximum rations'. The implication of hypothesis (a) is therefore that the food units are distributed over the sea-bed so that their local density is limited, although the supply of food is unlimited in that soon after a food unit is consumed it is replaced by another, thus tending to maintain the local density at a constant level.

The converse of hypothesis (a) is that there is a certain constant amount of food available to the population each year, the whole of which is consumed during the course of the year, irrespective of the abundance of the population, provided it lies within two limiting values which we have defined in §9.4.1. This assumption we shall refer to as *hypothesis* (c)*, and it will, admittedly, result in the prediction of an extreme variation of growth with population density, though if we have only limited data it may be of value for this reason alone. Hypothesis (c) is, in principle, similar to that put forward by Buckmann (1932), namely that the growth increment per fish is inversely proportional to the population abundance. Buckmann also introduced correction factors to take account of the maintenance and growth requirements and the varying efficiency of utilisation of food. That the total food consumption is constant is one of the limiting assumptions made also by Allen (1954) in his study of size limits and the size at first capture that gives the highest steady yield at a given fishing intensity.

Let us suppose that we wish to investigate, by means of hypothesis (c), the change in growth rate that will result from a change in the fishing mortality from one steady value to another. For this we require data referring to one equilibrium level of population density and growth rate, defined, say, by the observed values, ${}_1F$ and ${}_1W_\infty$. Putting these into (9.32) gives an estimate of Ξ which, according to the hypothesis, we regard as constant. With any proposed fishing mortality coefficient ${}_2F$, (9.32) contains two unknown quantities, the required growth parameter ${}_2W_\infty$ and the corresponding constant ${}_2t_0$. This latter may be expressed in terms of ${}_2W_\infty$ from (9.6), i.e.

$$
{}_2t_0 = t_\rho - \frac{1}{K}\log\left\{1 - \left(\frac{W_\rho}{{}_2W_\infty}\right)^{1/3}\right\}
$$

in which equation W_ρ and t_ρ can be taken as constants, since we are dealing with changes in growth of the post-recruit phase only. We have therefore only one unknown parameter, i.e. ${}_2W_\infty$, for which (9.32) provides a solution. Equation (9.32) can be used in an exactly comparable way to calculate the value of the parameter W_∞ resulting from a change in mesh size or in any other factor represented in the quantities $\bar{P}_{W^{2/3}}$ and $\bar{P}_W$, such as the annual recruitment. The equation can also be used to investigate the effect on the growth rate, and hence on the yield, of a postulated change in the supply of available food.

The remaining hypotheses which we shall put forward are concerned with elaborating the above methods in two directions; firstly, to take into account the variation in the intensity of feeding that is likely to occur with variation in the availability of food, and secondly, to introduce the influence of the grazing activity of fish on the abundance of the food organisms.

9.4.3.2.2 *Hypotheses* (d) *and* (e)*—the concept of 'hunger'*

Ivlev (1945) has discussed the problem of intensity of feeding, and criticises the methods of Lotka (1925) and Volterra (1928) which represent the degree of interaction between a predator and a prey population purely in terms of the frequency of contacts, with the rate of consumption of prey by a given stable predator population being directly proportional to the abundance of prey. F. E. Smith (1952) has made a similar criticism, that in these models "prey density has no effect upon the likelihood of a prey being eaten; there is no safety in numbers" (he suggests that this may be true if the predators are certain filter feeders, but even this seems doubtful), and also that neither the predatory species nor the prey ever inhibits *its own* growth. Ivlev suggests, on the contrary, that intensity of feeding (which is related to the proportion of contacts between predator and prey that result in the latter being eaten) will be proportional to the difference between the actual

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*In §18.4 where these hypotheses are tested, we shall refer to the empirical relationship between growth rate and population density discussed in §9.4.2, as *hypothesis* (b).

amount of food consumed per unit time by the animal and the maximum amount that would be consumed if food were in unlimited supply; in effect, to its *hunger*.* This leads him to express the amount of food consumed per unit time by an animal, i.e. the 'unit ration', by the equation

$$r = R(1 - e^{-kp}) \quad .. \quad .. \quad .. \quad .. \qquad (9.33)$$

where r is the actual 'unit ration', R is the maximal ration, p is the availability of the food, and k is a constant. In order to make use of Ivlev's concept in the present analysis we need to modify this equation to some extent.

Since we are dealing with a population comprised of individuals of a wide range of size, we require a definition of intensity of feeding that is applicable to a fish of any size. That this requirement is not satisfied by Ivlev's method can easily be seen by considering the intensity of feeding, as he defined it, by a large fish and by a small one. Thus, the *absolute* difference between the actual and maximal rations of a large fish might be considerably greater than between those of a small fish simply because of the greater magnitude of both rations of the large fish, and would not necessarily imply that the latter was feeding more intensely. We suggest that this difficulty might be resolved by defining the intensity of feeding in relative terms, as follows. Let us suppose that we have a fish of a given size, whose actual consumption of food per unit time can be denoted by ξ. If the maximum ration a fish of this size would consume is denoted by, say, ξ_L, then we shall define the intensity with which that fish is feeding by the expression

$$\frac{\xi_L - \xi}{\xi_L}$$

This definition can readily be extended to apply to the feeding intensity of a population. Thus, under stable conditions, we can replace ξ and ξ_L in the above expression by Ξ, the actual amount of food consumed by the population per year, and Ξ_L, the amount that would be consumed if an unrestricted supply of it were available. Hence the feeding intensity. of the population is given by

$$\frac{\Xi_L - \Xi}{\Xi_L}$$

Clearly, for this definition to be valid the annual food consumption of the population needs to be expressed by methods such as those of §9.4.3.1, which take into account its size composition and the growth rate of individuals comprising it. Thus Ξ in the above expression is given at once by (9.32), though some comment is required concerning the determination of Ξ_L. Let us suppose that the growth curve of a fish if supplied with unlimited food can be defined by a certain value of W_∞, say, $W_{\infty L}$. This value must not be confused with the 'theoretical' maximum possible $W_{\infty M}$, which could only be reached with an infinitely high rate of food consumption; in practice, $W_{\infty L}$ would usually be very much less than $W_{\infty M}$ and would be determined largely by physical factors which set a limit to the rate at which fish can consume food. For a particular population, Ξ_L is an abstraction in the same sense as is the concept of the maximum possible value of the annual net assimilated energy, $(1/k)_p$, and by an analogous argument is given by the equation

$$\Xi_L = \frac{1}{\varepsilon_0}\left\{(Q + 3KW_{\infty M}{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W\right\}\tanh^{-1}\left\{\frac{(Q + 3KW_{\infty L}{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}{(Q + 3KW_{\infty M}{}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}\right\} \qquad (9.34)$$

Our concept of $W_{\infty L}$ has a bearing on Medawar's (1945) distinction between a *limiting size* and a *stationary state*. Thus in a given set of environmental conditions our treatment of growth implies that the organism will approach a stationary state defined by a particular value of W_∞; that is, its size will tend towards a value that is constant and independent of time. In addition, we are also postulating a limiting value for this stationary state, which is attained when food is in abundant supply. The value of this limiting size depends upon the dimensions and general structure of the animal and, in particular, on its ability to consume and utilize food, and is defined by $W_{\infty L}$. Equation (9.34) therefore combines Medawar's two concepts.

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*That this concept of hunger can be given a definite physiological interpretation is shown by the work of Paintal (1953) on the impulses in vagal afferent fibres from stretch receptors in the stomach of cats.

Before we can develop equations giving the change of annual food consumption with population density, we need to define the 'availability of the food' referred to by Ivlev. This, of course, raises the difficulties already encountered with hypotheses (a) and (c), and a more detailed discussion of the problem is deferred until the following section. We may note, here, however, the expressions which are obtained if we make assumptions concerning the availability of food which are parallel to those made concerning its consumption in the first two hypotheses. Thus, following hypothesis (c), we may define the *total* food available to the population per year as constant, (*hypothesis* (d)). We can then write

$$\frac{d\Xi}{dt} = h_1\left(\frac{\Xi_L - \Xi}{\Xi_L}\right)$$

where h_1 is proportional to the amount of food available. Integrating from $t = 0$ to $t = 1$, we have the annual food consumption of the population given by the equation

$$\Xi = \Xi_L(1 - e^{-h_1/\Xi_L}) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (9.35)$$

To use this equation we require, as before, one observed level of population density and growth rate, from the data of which we may calculate an estimate of Ξ for these conditions by means of (9.32). To calculate Ξ_L from (9.34) we need also an estimate of $W_{\infty L}$ from experimental feeding data (see analysis of Dawes' data, §16.4.2). Inserting these in the above equation will then give an estimate of h_1. For any other value of the fishing mortality coefficient, mesh size, etc., the required value of W_∞ is that which gives new estimates of Ξ and Ξ_L that satisfy both sides of (9.35).

The implication of hypothesis (d) is that the total amount of food available each year is simply partitioned among the members of the fish population, each fish having access to one portion only. The amount that each fish eats of its portion is then determined solely by the intensity of feeding, as defined above. By analogy with hypothesis (a), on the other hand, we may define the food available to the population each year as proportional to the population numbers; *hypothesis* (e). This can be interpreted as implying that food is distributed over the sea-bed at a constant local density, but that as the numbers in the population increase, more food becomes available to it owing to the increased searching activity of the individual fish, this latter factor corresponding to the intensity of feeding. We can then put

$$\frac{d\Xi}{dt} = h_2\bar{P}_N\left(\frac{\Xi_L - \Xi}{\Xi_L}\right)$$

giving

$$\Xi = \Xi_L(1 - e^{-h_2\bar{P}_N/\Xi_L}) \quad \ldots \quad \ldots \quad \ldots \quad (9.36)$$

which can be used to solve for an unknown value of W_∞ as before.

9.4.3.2.3 *Hypothesis* (f)—*the dynamics of the food population and the problem of grazing*

Finally, for *hypothesis* (f), we attempt to incorporate in the population models the dynamic behaviour of both components of the predator-prey system. To establish the general methods, we retain in the first instance our previous assumption that the fish population in question is feeding on a single food species which can be treated as a homogeneous population.

The predatory activity of a fish population will result in a mortality in the food population which we shall call the *grazing mortality*, G. and there are several recorded instances of this mortality being very considerable. For example, work in the Limfiord (e.g. Blegvad, 1928) showed that large differences in the biomass of the food organisms in various areas were mainly attributable to the different densities of the plaice population; and detailed studies of the young sockeye salmon (*Oncorhynchus nerka*) of Cultus Lake B.C. and their predators, gave clear indication of the importance of predation in this community (see Foerster and Ricker, 1941, and Ricker, 1941). Other important examples of the effects of grazing by a fish population are given by Manteufel (1941), who showed that Barents Sea herring can produce severe local depletions of *Calanus*, and the experimental work of Ball and Hayne (1952) on the effects on the abundance of food organisms of removal of fish from lakes. From a theoretical point of view, the problem which presents the greatest difficulties is formulating an expression for the grazing mortality caused by a given fish population in terms of the characteristics of the latter and the abundance of the food population.

Basically, the *grazing power* of an individual fish, which is analogous to the fishing power of an individual vessel, must depend on establishing contacts with units of prey, these latter consisting of individual organisms or groups of organisms, as the case may be. The grazing power of a population will therefore depend, *inter alia*, on the number of individuals comprising it, and to our knowledge this is as far as the problem has been taken theoretically. We have previously mentioned that the methods of Volterra and Lotka assume that the grazing power of a population is directly proportional to the number of individuals comprising it, and the same procedure is followed by Riley (1947), for representing theoretically the grazing of a population of *Sagitta* on other zooplankton. When considering the grazing power of a fish population, however, there are other factors which must be taken into account. One of these is the variation of the grazing power of an individual fish with its size, since we shall need to evaluate the grazing power of populations in which the average size of fish differs considerably. This kind of variation can be regarded as resulting from the ability of larger fish to make a greater number of successful contacts with food units per unit time, perhaps because of their greater activity; it is a problem which could be investigated experimentally, though we know of no data of this kind for fish. The work of Gause, Smaragdova and Witt (1936) on the predation of *Paramoecium caudatum* by *Didinium nasutum* may, however, be cited here. From their fig. 6 (i) it can be seen that the specific consumption of a predator—which can be taken as an index of grazing power at a given prey density—is approximately proportional to its weight within the range of size investigated. Now, this weight is itself dependent on the previous rate of feeding, so that there is clearly a circular relationship here; as we shall show below, its consistent formulation requires that specific consumption be expressed as a function of the growth rate of the predators, as well as of their weight, if the growth is of the type found in fish—and probably in other cases also.

It is possible to make some appreciation of the problem by making use of certain facts concerning the growth of individuals comprising a natural population. As a starting point we shall take the general observation that growth in a fish population follows a definite pattern which under stable conditions remains fairly constant, as is true, for example, with the North Sea plaice. We now make two assumptions, the first being that there is no tendency for fish of particular sizes to be spatially segregated, so that all fish can be regarded as having access, over a period of time, to food units of the same local density: secondly, that either the food units are all the same size or, if this is not so, that over the range of sizes we are considering, large fish are no more, nor less, likely to consume large food units than are smaller ones. In these circumstances it follows that the amount of food consumed per unit time by fish of different sizes will be in the ratio of number of contacts with food units established by each fish, and hence in the ratio of their respective grazing powers.* If we then express the rate of consumption of food by a fish of a given weight and growth rate by the methods of §9.4.3.1 we have a means of expressing the grazing power of a fish in terms of its weight. Admittedly, these assumptions will never be precisely true, but they are likely to give a reasonably good generalisation, and the study of their implications indicates clearly the kind of data required to form a sound basis on which may be founded methods for assessing density dependent growth effects. The important point to note is that the variation of the grazing power of an individual with its body weight cannot be treated separately from the variation of the rate of growth and of the maintenance food requirements with body weight, and since the latter are the better known we have used them to deduce the former.

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*Again there is a direct analogy with fishing activity, since the method of determining the relative fishing powers of vessels discussed in §12 is to compare their catch per unit fishing time when all are fishing on the same density of population. The analogy breaks down, however, in that we must regard the grazing power of a fish of a given size as dependent on its growth rate; it is as if the fishing power of a vessel was dependent on the rate at which fish had been accumulating in its hold.

Another factor which must be considered is the variation in intensity of feeding with availability of the food, and since the intensity of feeding may be regarded as proportional to the fraction of the 'contacts' between a fish and the food units which result in the latter being eaten, the grazing power of a fish will be proportional to it. We have discussed this problem in connection with Ivlev's concept of 'hunger'* when putting forward hypotheses (d) and (e), and some further comments can be made at this point. If it is assumed that the grazing power of a fish is independent of the food supply, the implication is that it will eat a constant proportion of however much food is available to it. This is hardly acceptable when it is remembered that fish kept under experimental conditions will eat no more than a certain maximum daily ration; moreover, this ration is not so large that it could not reasonably be obtained in natural conditions (see §16.4), indicating that the grazing power of a fish must decrease as the availability of food increases and that the 'hunger' effect cannot be ignored in a theoretical treatment. (c.f. gear saturation, §8.3.2). It is interesting to find that in a number of animal population studies there is direct evidence of the action of factors limiting the grazing rate of a predator. Thus in the experiments of Harvey (1937), which were set up to measure the effect of grazing of *Calanus* on certain diatoms, there is evidence in the case of the fairly large diatom *Lauderia borealis* that the grazing rate increased as the abundance of the diatom decreased. The same is true of the experiments conducted by Pennington (1941) to study the grazing effect of *Daphnia pulex* on the alga *Diogenes rotundus*. In the experimental predator-prey system studied by Gause, Smaradgova and Witt (1936) the curve of specific consumption of prey (*Paramoecium caudatum*) by the predator (*Didinium nasutum*) against prey density was asymptotic, indicating a decrease of grazing mortality with increase of the ratio of prey to predators. On the other hand, the work of Gauld (1951) on the grazing of certain copepods on *Chlamydomonas* suggests that the grazing rate on this food did not vary within the range of density investigated, though this author does not present his data in a form that enables precise assessments to be made.

As in §9.4.3.2.2 we represent variation of the intensity of feeding with the availability of food by the ratio

$$\frac{\xi_L - \xi}{\xi_L} = 1 - \frac{\xi}{\xi_L}$$

so that denoting by g the coefficient of the grazing mortality caused by a fish, we can put

$$g \propto \xi\left(1 - \frac{\xi}{\xi_L}\right)$$

To define the grazing coefficient of a population, which we are denoting by G, it is only necessary to replace ξ and ξ_L by the food consumptions of the population, Ξ and Ξ_L, as determined by (9.32) and (9.34), so that we have

$$G \propto \Xi\left(1 - \frac{\Xi}{\Xi_L}\right) \quad \ldots \quad (9.37)$$

---

*Though strictly this word describes a subjective experience, it is conveniently used here as the complement of grazing intensity, despite the fact that it is only the amount of food consumed in the *immediate* past that conditions the feeling of hunger.

It is now possible to express the annual food consumption of a fish population as the 'yield' obtained by its grazing activity on the population of food organisms by means of the same general methods developed in Part I to relate yield to fishing activity. The precise form of such an equation will, of course, depend on the dynamic characteristics of the food population, but since these are seldom likely to be known in detail, we suggest the following simplifying assumptions which could be made:

(i) That the total annual recruitment, r, into the food population is not correlated with the size of the adult food population within the range of density changes of the latter with which we shall be dealing. The fact that a number of the more important species comprising the food of demersal fish, such as molluscs and polychaete worms, have a high fecundity and a pelagic larval stage, makes this reasonable as a working hypothesis.

(ii) That the growth of the food organisms during their grazeable life-span, λ', can be disregarded, reference being made to the mean weight, ω, during this time.

(iii) That 'natural' deaths, i.e. deaths due to all causes other than grazing by the fish population in question, can be assumed to take place at the end of the life-span only. In this way we can avoid having to specify a natural mortality rate, and can take some account of the effect of natural losses by an appropriate shortening of the life-span.

Clearly, for simplifications (ii) and (iii) to be satisfactory the main requirement is that the life-span of the food organisms should be short enough for the interaction between growth and mortality during their life not to have an important effect on their consumption by predators. This would seem to be a reasonable assumption, at least as far as invertebrate food species are concerned. Thus the approximate life-spans of molluscs comprising the food of plaice in Danish waters have been summarised by Boysen Jensen (1919), and range from one year in the case of *Nucula nitida* to several in the case of *Mya truncata*.* Definite evidence could not be obtained for polychaetes, but Boysen Jensen took them to have a life-span of one year, and it would seem that the average life-span of the important food organisms would probably be between one and two years. Birge and Juday (1922), in a study of the productivity of lakes, were content to assume that species spending more than one year in the aquatic stage balance those having a number of generations in one year. According to Macan and Worthington (1951), this is now general practice among limnologists. There is some indication that the annual growth of North Sea haddock is influenced to a small extent by their density in the preceding year (see §16.4.1.2). This suggests that the effective life-span of the food organisms concerned is between one and two years, but the influence was slight and could not be detected when the whole of the data was analysed.

The methods of §4 can now be used to obtain the annual food consumption of a population in the form

$$\Xi = G\,.\,r\omega\int_0^{\lambda'} e^{-G\,.\,\psi}\,d\psi$$

$$= r\omega(1 - e^{-G\lambda'}) \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (9.38)$$

and we shall show later that it is possible to obtain estimates of the products $r\omega$ and $G\lambda'$ (and hence to evaluate Ξ) without direct information about the dynamics of the food population. If the 'natural' mortality of the food organisms is appreciable, a better expression for Ξ would be

$$\Xi = \frac{G\,.\,r\omega}{G + m'}\left(1 - e^{-(G + m')l}\right)$$

where m' is the 'non-grazing' mortality coefficient and l is the 'true' life-span of the food organisms. However, the value of m' would usually be difficult to estimate directly, in which event (9.38) can provide a reasonably close approximation to Ξ. Thus if it is employed in this case it amounts to using the quantity

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*Boysen Jensen mentions that specimens of *Mya* above a certain age are too large to be eaten by plaice, so that even here the effective life-span is relatively short.

$$\frac{1 - e^{-G\lambda'}}{G}$$

as an approximation to

$$\frac{1 - e^{-(G + m')l}}{G + m'}$$

Now, for any given value of G there is a value of λ' which will result in these two expressions being identical, and in practice this value of λ' would be determined to satisfy this condition from an observed initial state, as described below. For other values of G the use of this value of λ' in (9.38) will give a reasonably close estimate of Ξ unless m' is very large, the tendency being for changes in Ξ with G to be underestimated. A case where the grazing mortality caused by fish predation is only a small fraction of the total losses in a food population is provided by the studies of Borutsky (1939) on the dynamics of *Chironomus plumosus* of Lake Beloe.

Another possibility which may arise is that although the non-grazing mortality is not large there is nevertheless appreciable grazing by fish populations other than the one in question. In general this is best regarded as a problem of competition between two or more predators for a common food supply, and is discussed briefly in this connection in §11.2.1. It is worth noting, however, that if all the fish predators are caught together by the same gear, (9.38) again gives a reasonable approximation to the food consumption of the fish population which is being examined. In this case the latter can be assumed to generate a constant fraction x of the total grazing mortality, and its food consumption becomes

$$\Xi = x \, . \, r\omega(1 - e^{-G\lambda'/x})$$

The parameters estimated from data are now $x \, . \, r\omega$ and $G\lambda'/x$ instead of $r\omega$ and $G\lambda'$, but since x does not need separate evaluation, this equation gives the same kind of relationship between Ξ and G. The application of (9.38) in this way to the evaluation of the food consumption of North Sea plaice, which has several competitors exploited by the same fishing activity, is described in §18.4.2.4.

Despite the simplified nature of (9.38)* it would nevertheless seem that it will give a satisfactory representation in many instances of the relationship between grazing power of a fish population and amount of food consumed by it, and we shall now consider the kind of information which is required to use it. If nothing is known about the behaviour of the food population, but data for two steady levels of density of the fish population and the corresponding growth rate are available, we may proceed as follows. From the first of these levels we can observe a value ${}_1W_\infty$ (say), and calculate the annual food consumption ${}_1\Xi$ by means of (9.32) in the usual way, and we can therefore write

$${}_1\Xi = r\omega(1 - e^{-{}_1G\lambda'}) \quad .. \quad .. \quad .. \quad (9.39)$$

Similarly, for the second level, we observe a value ${}_2W_\infty$, and calculate ${}_2\Xi$; in this case, making use of (9.37) we can put

$${}_2\Xi = r\omega(1 - e^{-{}_2u \cdot {}_1G\lambda'}) \quad .. \quad .. \quad .. \quad (9.40)$$

---

*There are, of course, certain other factors which might need to be taken into account if detailed studies were being made. For example, the use of the simple equation (9.38) implies that the benthic populations are in a state of flux, there being either a more or less continuous recruitment from the pelagic stage filling 'gaps' made by locally intense grazing, or a movement of adult animals over the bottom tending to have the same effect of restoring the initial distribution. Moon (1940) has produced direct evidence that this latter occurs in fresh-water, and concludes that . . . "the fauna moves about freely over the substratum and colonises bare areas". Nevertheless, aggregation of food organisms may often be appreciable; an extension of the above methods to cover one aspect of this problem, namely, the effects of an aggregated food on the efficiency of its utilisation by fish, is discussed briefly in §9.4.3.3.

where

$$ {}_2u = \frac{{}_2\Xi\left(1 - \dfrac{{}_2\Xi}{{}_2\Xi_L}\right)}{{}_1\Xi\left(1 - \dfrac{{}_1\Xi}{{}_1\Xi_L}\right)} $$

and ${}_1\Xi_L$ and ${}_2\Xi_L$ can be calculated for each level respectively by means of (9.34). Equations (9.39) and (9.40) provide a solution for the quantities $r\omega$ and ${}_1G\lambda'$, and for any other level of population density we have

$$ {}_x\Xi = r\omega(1 - e^{-{}_xu\cdot{}_1G\lambda'}) \quad \ldots \quad \ldots \quad \ldots \quad (9.41) $$

where

$$ {}_xu = \frac{{}_x\Xi\left(1 - \dfrac{{}_x\Xi}{{}_x\Xi_L}\right)}{{}_1\Xi\left(1 - \dfrac{{}_1\Xi}{{}_1\Xi_L}\right)} $$

in which the only unknown quantity is ${}_xW_\infty$ appearing in the equations for ${}_x\Xi$ and ${}_x\Xi_L$, and for which a solution can therefore be obtained.

It will be appreciated that the accuracy with which it is possible to represent the behaviour of the food population depends on the type of data available, and the simplifying assumptions detailed above have been made in order to reduce the requisite data to the minimum. For example, if data from only one equilibrium level of density of the fish population were available, it would be necessary to know something of the characteristics of the food population for ${}_xW_\infty$ to be the only unknown parameter of (9.41). One characteristic that it might be possible to determine in these circumstances is the annual mean biomass of the food population, or, in effect, its *standing crop*, $\bar{p}_W$, and another—perhaps with the help of tank experiments—is the life-span, λ'. Now, since standing crop bears the same relationship to Ξ as does biomass of the exploited phase of a fish population to yield, we can put

$$ {}_1G = \frac{{}_1\Xi}{{}_1\bar{p}_W} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (9.42) $$

and substituting in (9.38) gives

$$ r\omega = \frac{{}_1\Xi}{1 - e^{-\lambda'({}_1\Xi/{}_1\bar{p}_w)}} \quad \ldots \quad \ldots \quad \ldots \quad (9.43) $$

One further case worthy of mention is that in which data for two levels of fish density are available, and also indices of the corresponding standing crops but not the absolute values. In addition to (9.39) and (9.40) above, we should have in this case

$$ \frac{{}_1\bar{p}_W}{{}_2\bar{p}_W} = {}_2u\left(\frac{1 - e^{-{}_1G\lambda'}}{1 - e^{-{}_2u\cdot{}_1G\lambda'}}\right) \quad \ldots \quad \ldots \quad \ldots \quad (9.44) $$

where ${}_2u$ is defined as before, the three equations providing solutions for $r\omega$, ${}_1G$, and λ'. Alternatively, if we regard ${}_1G\lambda'$ as a single quantity, these equations provide a solution for ${}_2u$, and hence offer a means of testing the applicability of (9.37) to the relation between the grazing power of a population and its structure and size-composition.

9.4.3.2.4 *Grazing on two or more foods*

When formulating hypothesis (f) it was assumed that the fish population was feeding on a single species or type of food organism. The previous hypotheses did not require this assumption, though only because the behaviour of the food populations was not represented by them in sufficient detail. The method used to develop hypothesis (f) can, however, be extended to an analysis of the case in which fish are feeding on more than one species of food organism, provided there is no appreciable interaction between the latter.

Many studies on the feeding habits of fish, of which we may mention those of Todd (1915) and Blegvad (1926) for the plaice, have shown that if different species of fish inhabit the same area, the proportion of the various organisms comprising their food is usually different for each of them. This fact leads to the conclusion that, in general, a fish species grazes different types of food at different intensities. Blegvad has in fact shown that different densities of a plaice population could completely alter the composition of the bottom fauna. Since populations of different species of food organisms are likely to differ considerably in their abundance and also in their nutritional value, the case of a fish population feeding on a heterogeneous food supply is likely to differ sufficiently from the simple situation discussed in the previous section to merit separate treatment.

For the following analysis we assume that the fish in question feed on two species of food organisms, A and B, since the same methods can easily be extended to an analysis of feeding on more than two species. Denoting the parameters of food species A by the suffix $_A$, and those of food B by the suffix $_B$, the annual food consumption of the population, with the assumptions of the previous section, can be written as

$$\Xi_{AB} = \Xi_A + \Xi_B = (r\omega)_A (1 - e^{-G_A \lambda'_A}) + (r\omega)_B (1 - e^{-G_B \lambda'_B}) \quad .. \quad (9.45)$$

In order to relate Ξ_{AB} of (9.45) to the maintenance and growth requirements of the fish population we need to take into account the difference in nutritional value of the two food species, which may be considerable in the case of molluscs and worms, for example. One way in which this can be done is to define the maximum value of the efficiency of utilization of food, ε_0, with reference to, say, the favourite food A, and find by experiment the number of grams of food B required to produce the same rate of growth, in a fish of the same size, as 1 gm. of food A. In this way we can obtain a direct measure of the relative nutritional values of the two foods in the form we require without attempting an analytical investigation of their biochemical nature. If we denote this amount of food B as $1/{}_A\nu_B$, then ${}_A\nu_B$ can be called the *nutritional factor* of food B with respect to food A, and the equivalent annual food consumption in terms of food A becomes

$$\Xi'_{AB} = \Xi_A + {}_A\nu_B \cdot \Xi_B \quad .. \quad .. \quad .. \quad (9.46)$$

It is this quantity Ξ'_{AB} which will be obtained from (9.32) using the observed growth rate of the population and the value of ε_0 for food A.

The next problem arising is that of expressing the grazing power of a fish in terms of its food consumption and intensity of feeding (i.e. by equations similar to (9.37)) when two foods are involved. From the discussion of §9.4.3.2.3 it follows that the dependence of the grazing power of a fish on its size and growth rate should be expressed by putting both G_A and G_B proportional to the gross energy consumption, i.e. to Ξ'_{AB} of (9.46). Similarly, the intensity of feeding of a fish is by definition the same on both foods, but with two foods of differing nutritional value the question arises whether the limiting consumption is better expressed in terms of bulk or gross energy. Relevant here is the evidence that in some species of fish, at least, food is normally taken as a series of discrete meals, each being digested before the next is taken in (see §9.4.3.3). Thus it would be expected that bulk would be the main factor limiting the size of each meal, as is indicated by Raymont's (1947) study on the feeding of flounders (*Pleuronectes flesus*) of Loch Craiglan. He showed that at a time when the fish were feeding to capacity on molluscs (mainly *Cardium*) the dry-weight of organic material in the stomach was not as high as when the food consisted largely of chironomids. On the other hand, a meal of food with a high dry-weight content of organic material—which in a general sense can be taken as indicating a high energy content and nutritional value—would be expected to take longer to digest than a meal of the same size with a low energy content. This would have the effect of making, over a period, the limit of consumption in bulk of a food of low energy content somewhat greater than that of a highly nutritional food, thus tending to reduce the difference between the net amounts of energy assimilated from the two foods.

It is clear that the relative importance of bulk and gross energy in determining the limit of food consumption is a question readily answered experimentally. In order to continue with the theoretical treatment of a mixed food supply we shall here suppose that the limiting amount of gross energy a fish of a given size would take if presented with an unlimited supply of food does not depend on the type of food, and indicate at the end of this section the modifications required when this is not so. Consequently we can write

$$\Xi_{LA} = {}_A\nu_B \,.\, \Xi_{LB} = \Xi'_L$$

and define a unique value of $W_{\infty L}$ corresponding to the limiting gross energy consumption Ξ'_L. Thus we have

$$G_A \text{ and } G_B \text{ both} \propto \Xi'_{AB}\left(1 - \frac{\Xi'_{AB}}{\Xi'_L}\right)$$

Now, the difference between the magnitudes of G_A and G_B arises from that between the constants of proportionality which, in these expressions, define the *grazing efficiencies* of the fish population on the two foods. Thus the two grazing mortality coefficients may differ because of a deliberate preference on the part of the fish for one food rather than the other, and also because the vulnerabilities of the two food organisms are different, that is, because they differ in their ability to avoid sensory contacts with fish or to avoid capture after contact has been made. The implications of differences in preference and vulnerability are discussed further in §9.4.3.2.5; here it is sufficient to refer to their combined effect in terms of the grazing efficiency on each food, and put

$$G_A = S_A \,.\, \Xi'_{AB}\left(1 - \frac{\Xi'_{AB}}{\Xi'_L}\right) \quad \ldots \quad \ldots \quad \ldots \quad (9.47)$$

and

$$G_B = S_B \,.\, \Xi'_{AB}\left(1 - \frac{\Xi'_{AB}}{\Xi'_L}\right) \quad \ldots \quad \ldots \quad \ldots \quad (9.48)$$

where S_A and S_B are constants defining the grazing efficiency on foods A and B respectively. Denoting by ${}_AS_B$ the efficiency of grazing on food B, relative to food A ($= S_B/S_A$), and dividing (9.47) by (9.48) gives

$$G_B = {}_AS_B \,.\, G_A \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (9.49)$$

With these expressions and (9.45), it is possible to express (9.46) in a form analogous to (9.41) for a single food. Thus if it is supposed that the above equations refer to an observed level of density of the fish population then for any other level we have

$${}_x\Xi'_{AB} = (r\omega)_A(1 - e^{-{}_xu \,\cdot\, {}_1G_A \,\cdot\, \lambda'_A}) + {}_A\nu_B(r\omega)_B(1 - e^{-{}_xu \,\cdot\, {}_AS_B \,\cdot\, {}_1G_A \,\cdot\, \lambda'_B}) \quad \ldots \quad (9.50)$$

where

$${}_xu = \frac{{}_x\Xi'_{AB}\left(1 - \dfrac{{}_x\Xi'_{AB}}{{}_x\Xi'_L}\right)}{\Xi'_{AB}\left(1 - \dfrac{\Xi'_{AB}}{\Xi'_L}\right)} \quad \ldots \quad \ldots \quad \ldots \quad (9.51)$$

The equations of this section can be used to obtain the growth rate in the fish population, i.e. the value of ${}_xW_\infty$ appearing in the equations for ${}_x\Xi'_{AB}$ and ${}_x\Xi'_L$, in similar ways to those described for hypothesis (f) in the previous section, except that rather more data are required. It is now practically essential to have data referring to the relative abundance of the two food species. Thus, the ratio of the annual mean standing crops of the two foods is

$$\frac{\bar{p}_{WA}}{\bar{p}_{WB}} = \frac{{}_AS_B \cdot (r\omega)_A(1 - e^{-G_A\lambda'_A})}{(r\omega)_B(1 - e^{-{}_AS_B \cdot G_A\lambda'_B})}$$

so that, from (9.50) we can write

$$ {}_x\Xi'_{AB} = (r\omega)_A(1 - e^{-x^u \cdot G_A\lambda'_A})\left\{1 + {}_A\nu_B \cdot {}_AS_B\left(\frac{\bar{p}_{WB}}{\bar{p}_{WA}}\right)\right\} \quad .. \quad (9.52)$$

If we do not know the nutritional factor ${}_A\nu_B$, or the relative grazing efficiency, ${}_AS_B$, this equation in effect contains three unknowns, viz.: $(r\omega)_A$, $G_A\lambda'_A$ and ${}_A\nu_B \cdot {}_AS_B$ assuming, of course, that we know the ratio $\bar{p}_{WB}/\bar{p}_{WA}$. Consequently, with data for growth rate and relative standing crops for three equilibrium levels of fish abundance, three values of ${}_x\Xi'_{AB}$ can be calculated from (9.32) and estimates obtained for the unknowns listed above. On the other hand, it may be possible to obtain independent estimates of ${}_A\nu_B$ and ${}_AS_B$, in which case we require data referring to two equilibrium levels in order to obtain $(r\omega)_A$ and $G_A\lambda'_A$. Thus ${}_A\nu_B$ may be determined by feeding experiments, as mentioned above, though some comment is required concerning the experimental determination of ${}_AS_B$.

If grazing by the fish population in question is the sole cause of mortality in both food species, as we have been assuming, then

$$\frac{dn_B}{dn_A} = {}_AS_B \frac{n_B}{n_A}$$

where n_A and n_B are indices of abundance of the two foods at any time. Solving this equation and taking logarithms gives the linear equation

$$\log n_B = {}_AS_B \,.\, \log n_A + \log C \quad .. \quad .. \quad .. \quad (9.53)$$

in which C is a constant. Plotting a series of values of $\log n_B$ against $\log n_A$ taken at various times during the year, the slope of the regression provides an estimate of the relative grazing efficiency ${}_AS_B$. Clearly, it is necessary that there should be no recruitment to the food populations during the period in which the values of n_A and n_B are being obtained.

Another method of determining the relative grazing efficiency ${}_AS_B$ is to make use of stomach content analyses. From (9.45) the annual consumption of the two foods is given as

$$\Xi_A = (r\omega)_A(1 - e^{-G_A\lambda'_A}) \quad .. \quad .. \quad .. \quad (9.54)$$

and

$$\Xi_B = (r\omega)_B(1 - e^{-{}_AS_B \cdot G_A\lambda'_B}) \quad .. \quad .. \quad .. \quad (9.55)$$

while the annual mean standing crops are

$$\bar{p}_{WA} = \frac{(r\omega)_A}{G_A}\left(1 - e^{-G_A\lambda'_A}\right)$$

and

$$\bar{p}_{WB} = \frac{(r\omega)_B}{{}_AS_B \cdot G_A}\left(1 - e^{-{}_AS_B \cdot G_A\lambda'_B}\right)$$

From these equations

$$\frac{\Xi_A}{\Xi_B} = {}_AS_B \frac{\bar{p}_{WA}}{\bar{p}_{WB}} \quad .. \quad .. \quad .. \quad .. \quad (9.56)$$

Estimates of the quantity Ξ_A/Ξ_B might be obtained by observing the ratio of the two foods in the stomachs of the fish during the year and taking an average value, allowance being made for any difference between the rates at which they are digested, by methods such as those developed by Hess and Rainwater (1939). If values of the annual mean standing crops of the two foods are also available, the relative grazing efficiency can be estimated.

Finally, some comment is required on the assumption that the limiting consumption of gross energy is independent of type of food. The modifications of the above treatment that are necessary when this is not the case are best shown by assuming alternatively that the consumption of food is limited purely by bulk, since it will be sufficient for practical purposes to use whichever of these two assumptions is most nearly in accordance with what happens in feeding experiments. When bulk limits consumption, intensity of feeding is defined by the extent to which the actual consumption in bulk of both foods, Ξ_{AB}, falls short of the limiting consumption $\Xi_{L\,AB}$; hence instead of (9.47) and (9.48) we have

$$G_A = s_A \Xi'_{AB}\left(1 - \frac{\Xi_{AB}}{\Xi_{L\,AB}}\right)$$

$$G_B = s_B \Xi'_{AB}\left(1 - \frac{\Xi_{AB}}{\Xi_{L\,AB}}\right)$$

and it will be seen that, as before,

$$G_B = {}_AS_B \,.\, G_A$$

Hence (9.50) is unchanged except that ${}_xu$ of (9.51) is now given by

$${}_xu = \frac{{}_x\Xi'_{AB}\left(1 - \dfrac{{}_x\Xi_{AB}}{{}_x\Xi_{L\,AB}}\right)}{{}_1\Xi'_{AB}\left(1 - \dfrac{{}_1\Xi_{AB}}{{}_1\Xi_{L\,AB}}\right)} \qquad \ldots \quad \ldots \quad \ldots \quad (9.57)$$

In this expression the limiting consumption in bulk of both foods together, $\Xi_{L\,AB}$, and the corresponding growth parameter $W_{\infty\,L}$, would be determined as before by feeding experiments. In this case the fish are presented with excess of both foods roughly in the proportion of their occurrence in nature, since if their nutritional values differ, $W_{\infty\,L}$ depends on the proportion in which they are taken by the fish. The quantities Ξ_{AB} and ${}_x\Xi_{AB}$, unlike their counterparts Ξ'_{AB} and ${}_x\Xi'_{AB}$ of (9.51), cannot be estimated from a knowledge of the growth and structure of the fish population since they refer to bulk of food and not to its nutritional value. Remembering that $\Xi_{AB} = \Xi_A + \Xi_B$, a relation between Ξ_{AB} and Ξ'_{AB} can, however, be found from (9.46) and (9.56), i.e.

$$\Xi_{AB} = \frac{\Xi'_{AB}}{{}_A\nu_B + \dfrac{\bar{p}_{wA}}{\bar{p}_{wB}} \,.\, {}_AS_B}\left(1 + \frac{\bar{p}_{wA}}{\bar{p}_{wB}} \,.\, {}_AS_B\right)$$

If this expression for Ξ_{AB} is substituted in (9.57) for u_x to be used in (9.50), it will be seen that no new parameter is involved, except that it is now necessary to know ${}_A\nu_B$ and ${}_AS_B$ separately whereas before they appeared only as the product ${}_A\nu_B \,.\, {}_AS_B$. This means that independent estimates of either or both these parameters, by methods such as those outlined above, are now virtually essential, but the procedure for using (9.50) is otherwise unchanged.

It will be noted that the modifications of the above treatment of grazing on a mixed food supply that are needed when there is an appreciable non-grazing mortality in either food species, or if they are grazed by other fish populations, are similar to those discussed in connection with grazing on a single food species in §9.4.3.2.3. Certain aspects of the treatment are not, however, affected by such complications, notably the use of (9.56) to estimate the relative grazing efficiency ${}_AS_B$, and the discussion of preference and vulnerability in the following section.

9.4.3.2.5. *Evaluation of food preferences and vulnerability*

One consequence of attempting to set up a theoretical model representing the grazing of a fish population on a mixed food supply is that it has shown the kind of information that is needed, from feeding experiments and samples of the food species, for a full interpretation of changes in growth and density of the fish. Of particular interest are certain implications of our treatment concerning the relationship between the proportion of the two foods on the grounds and the proportion eaten by fish. The above methods have a bearing on a problem which is of considerable importance in ecological studies on feeding relationship, namely the measurement of the preference of fish for the various food organisms which are available to it. The index usually employed is the ratio of the percentage of the food in question in the stomach contents to the percentage which that food comprises of the total fauna in the feeding area of the fish (Larsen, 1936). This ratio has been variously termed the "index of food preference" (Shorygin, 1939), the "forage ratio" (Hess and Swartz, 1941), and the "availability factor" (Allen, 1941a). A similar index based on a points system has been used by Hynes (1950), who gives a review of the literature on this subject.

To interpret this index in our terms we may suppose that it is estimated for a particular organism, A, present in both the food and the fauna, and denote its value by "*A*". The remaining organisms present in the stomach contents can be denoted by B, C, etc. . . . Z, and those comprising the fauna as B′, C′ . . . etc. . . . Z′, where in the general case Z will not be the same as Z′ because certain components of the fauna may be entirely absent from the food. By the previous methods it is then possible to write

$$\text{Consumption of food A} = \Xi_A = (r\omega)_A (1 - e^{-G_A \lambda'_A})$$

$$\text{Total food consumption} = \Xi = \sum_{x=A}^{Z} (r\omega)_x (1 - e^{-G_x \lambda'_x})$$

$$\text{Standing crop of food A} = \bar{p}_{W_A} = \frac{(r\omega)_A}{G_A}\left(1 - e^{-G_A \lambda'_A}\right)$$

$$\text{Total standing crop} \qquad = \bar{p}_W = \sum_{x=A}^{Z'} \frac{(r\omega)_x}{G_x}\left(1 - e^{-G_x \lambda'_x}\right)$$

The index for food A is therefore

$$\text{“}A\text{”} = \frac{\dfrac{\Xi_A}{\Xi}}{\dfrac{\bar{p}_{W_A}}{\bar{p}_W}} = G_A \cdot \frac{\displaystyle\sum_{x=A}^{Z'} \frac{(r\omega)_x}{G_x}\left(1 - e^{-G_x \lambda'_x}\right)}{\displaystyle\sum_{x=A}^{Z} (r\omega)_x (1 - e^{-G_x \lambda'_x})} = G_A \cdot \frac{\bar{p}_W}{\Xi} \quad \ldots \quad \ldots \quad (9.58)$$

and is thus seen to be proportional to the grazing mortality coefficient in food A, the constant of proportionality being the ratio of the total standing crop to the total food consumption.

Now with a set of observations taken over a short period it might be possible to treat the ratio $\bar{p}_W/\Xi$ as constant, in which case the indices "*A*", "*B*" . . . etc. computed by the above method will be in the ratios of the grazing mortality coefficients on the various foods. The particular numerical values of the indices will have no absolute significance, however, and they cannot be compared or combined with estimates obtained at other times or places, since the total standing crop $\bar{p}_W$ and the total food consumption Ξ will almost certainly differ. It can similarly be shown that the *index of electivity*, E, which Ivlev (1946) has proposed as a substitute for the index "*A*", suffers from the same defect in that its magnitude might also be expected to vary according to the relative composition of the total food supply. This particular difficulty can be overcome by restricting analysis to the set of organisms that is consistently present in both the food and fauna throughout the range of observations, and expressing the index for each food as a fraction of the sum of the indices.

This procedure results in derived indices giving the grazing mortality coefficient on each food as a fraction of the total grazing mortality on all the foods in question; it thus gives a picture of the relative distribution of grazing activity on those particular foods that is not invalidated by variations in the magnitude or composition of the remaining part of the total food or fauna.

The question remaining is whether an index which is proportional to the grazing mortality coefficient in a particular food can be used as a measure of the preference for that food. The problem evidently hinges on the precise definition of preference, which does not seem to have been put forward hitherto. Fundamentally, we may suppose that when an animal is confronted with a particular kind of food organism it has the choice of two possible procedures—acceptance or rejection. The degree of preference for that food could therefore be defined as the proportion of contacts with it that result in acceptance, a value which will bear a direct relationship to the grazing mortality coefficient generated in a population of food organisms of that kind. In practice, however, the preference for a food measured in this way depends on the intensity with which the animal is feeding, i.e. on its 'hunger', and therefore will vary according to the contemporary abundance of the total food supply available to it. A more useful procedure is therefore to define preference in relative terms as the ratio of the proportion of contacts with a standard food A that result in acceptance to that of food B, the two foods being simultaneously available to the fish so that the intensity of feeding on each is the same. This ratio could be determined directly by means of tank experiments, but field observations on the abundance of the two foods in the bottom fauna and in the stomach contents can only give a measure of preference if the two foods are *equally vulnerable*, that is, if the number of contacts made per unit time by the fish with the two foods is in the same ratio as their true abundances, and that the chance of each of the two food organisms avoiding capture following a contact with a fish is the same. If these conditions are satisfied, the relative preference is given by the ratio of the grazing mortality coefficients in each food population. This ratio is, of course, the parameter ${}_AS_B$, which we have called the relative grazing efficiency because in the general case its value will depend on the relative vulnerability of the two food organisms as well as on the preference for one over the other. Thus from (9.56) we have

$${}_AS_B = \frac{\Xi_B}{\Xi_A} \cdot \frac{\bar{p}w_A}{\bar{p}w_B} \quad .. \quad .. \quad .. \quad .. \qquad (9.59)$$

The practical implication of the above discussion is that observations on the composition of stomach contents and fauna can give only the relative grazing mortalities in the food species. Moreover, if the latter are to be compared at different times and places, analysis must be restricted to those species which are present in both the stomach contents and the fauna throughout the range of observations. The distinction between the parts played by preference and vulnerability is a problem seldom likely to be solved except by recourse to experiment. For example, it might be possible to measure the preferences for a series of foods by presenting them to the fish so that it has an equal opportunity of consuming each; comparison with the relative grazing mortalities of those foods computed from field observations would then give estimates of their relative vulnerability.

There are some further conclusions which may be drawn from our treatment of grazing on a mixed food supply. It will be noticed from (9.54) and (9.55) that as the abundance of the fish population increases, i.e. as G_A increases, we have

$$\frac{\Xi_A}{\Xi_B} \rightarrow \frac{(r\omega)_A}{(r\omega)_B}$$

that is, the ratio of the amounts of the two foods consumed approaches the ratio of the yearly influx to the food populations. Conversely, as G_A decreases, we have

$$\frac{\Xi_A}{\Xi_B} \rightarrow {}_AS_B \frac{(r\omega)_A}{(r\omega)_B}$$

so that as the density of the fish population decreases, fish tend to eat a smaller proportion of the less easily captured or less favoured food, and this behaviour is in accordance with data. For example, Allen (1941a) found that the percentage of the dominant food organism in stomachs of young salmon increased as the number of animals in the stomachs increased, i.e. as the food supply became more plentiful.* The work of Ricker (1941) on the grazing by predatory fish on the population of young sockeye salmon in Cultus Lake showed that when the latter were abundant they formed practically the whole of the food of the predators, but when the salmon were scarce the predators greatly increased their consumption of other foods. For the present purposes it is permissible to take again the case of two foods, and denote the sockeye by A and the remaining food organisms by B. Then from (9.56), if we suppose $\bar{p}_{W_A}$ decreases, the ratio of the consumption of sockeye to that of other foods will change in favour of the latter. This accounts for part of the effect observed by Ricker, but in addition he found that the *absolute* consumption of other foods, i.e. Ξ_B, increased when there were few sockeye. Now the magnitude of Ξ_B (assuming recruitment to the foods B stays constant) depends on the value of the grazing mortality coefficient G_B as given by (9.55), but when the abundance of sockeye decreases it means that the total food supply to the predator has decreased. According to our treatment their general intensity of feeding will therefore increase as a result of their greater 'hunger', and hence the value of G_B as defined by (9.37) will increase. The result of this will be an absolute, as well as a relative, increase in the consumption of foods B, which is the phenomenon observed by Ricker. If the conditions of low sockeye abundance persisted for a long period, G_B might be expected to fall owing to a smaller average size of the predators resulting from their slower growth, but in the case investigated by Ricker the abundance of sockeye changed greatly from year to year.

An important feature of our treatment is the assumption that the relative grazing efficiency ${}_AS_B$ of a given species of fish on any two particular foods A and B is constant; since this ratio includes any preference there may be for one food relative to the other it implies also that this preference remains independent of the abundance and composition of the food supply. This would seem to be a reasonable assumption, and from the above discussion it would appear to give conclusions which are at least in general accordance with observation. A more critical test of whether preference does remain independent of the composition of the food supply would be to compute relative grazing efficiencies from data of food consumption and standing crop covering a fairly wide range of values of the latter and in which the relative vulnerability of foods is likely to stay fairly constant.

The work of Neill (1938) on the food and feeding of brown trout (*Salmo trutta* L.) in the River Don provides data which, though not extensive, nevertheless meet these general requirements. He showed that the four main groups of organisms in both the food and fauna during the feeding period when the observations were made were *Simulium* larvae, *Simulium* pupae, larvae of Trichoptera and nymphs of Ephemeroptera. The relative and absolute abundances of these in the feeding area of the trout varied considerably during the four months April-July, the numbers per 1000 sq. cm. in each month being given in columns A-D of Table 9.1. Neill sampled the trout population regularly during the period, and although he does not specifically conclude that the abundance of fish was constant, the uniformity of the catches suggests that this was so at least to a first approximation. The average numbers of organisms of the above groups per stomach in each month can therefore be taken as an index of the total consumption of those organisms, and are given in columns E-H of the same table. An index of the grazing mortality coefficient for each food in each month can now be computed from (9.58) as the ratio of the numbers per stomach to the numbers per 1000 sq. cm., and these are plotted against time in Fig. 9.1.

The main feature of Fig. 9.1 is that although the grazing mortality indices change considerably during the period, their relative magnitudes remain comparatively stable. The only anomaly is in the Ephemeroptera (d), where there is a high grazing mortality index

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*Allen concluded that the relationship between the percentage of the dominant and the number of animals in the stomach was in two separate phases, but his data are, in fact, fitted well by a single curve rising to an asymptote, as would be expected from the above theory of grazing.

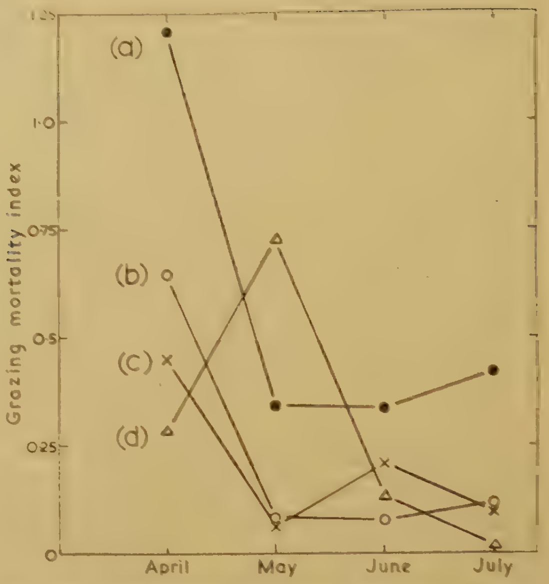

FIG. 9.1 GRAZING MORTALITY CAUSED BY TROUT

[Mortality indices in four species of trout food plotted against time; data from Neill (1938) and Table 9.1. (a) = *Simulium* pupae, (b) = *Simulium* larvae, (c) = Trichoptera larvae, (d) = Ephemeroptera nymphs. In the first three of the species the trends follow nearly the same course, indicating that the relative grazing mortality coefficients are roughly constant.]

in May, followed by an equally marked decline in the two succeeding months. In this connection Neill points out that . . . "The dominant species in spring is *Baëtis rhodani* Pict., rivalled from the end of May onwards by *Ephemerella ignita* Poda". Furthermore, Neill found that the increase in abundance of Ephemeroptera in June and July was due largely to emergence of young nymphs which can find good shelter among the finer substratum. Thus the Ephemeroptera material is heterogeneous as far as vulnerability is concerned (and possibly preference also) and for this reason cannot be taken as conflicting evidence. Bearing in mind the large changes in the absolute and relative abundances of the foods, these data lend support to our treatment of grazing on a mixed food supply as a more or less random process, with such preferences as may exist being effectively independent of the composition of the food supply. A preliminary analysis of Allen's (1941a) data for young salmon in the Rivers Eden and Thurso gives a substantially similar result when the relative grazing efficiencies referring to the different tributaries of these rivers, in which the faunal abundance and composition varies, are compared. N. S. Jones (1952) gives data that make it clear that the feeding of plaice conforms to this type of pattern. Qualitatively the food (from gut contents) and fauna (grab samples) correspond, plaice being rather general feeders in comparison with, for example, dabs, but not so unselective as the tactile feeding sole. Quantitative analysis shows, however, that the relative grazing efficiencies vary from one food to another, and the author concludes that "plaice almost certainly select their food".

Another interesting point concerning the indices of Fig. 9.1 is their trend with time. Neill concludes that the paucity of food in the stomachs during April was a reflection of the sluggishness of the fish, and suggests that this was due to the low water temperature of that month. On the other hand, Fig. 9.1 shows that the grazing mortality indices for all foods except the Ephemeroptera (see previous paragraph) were highest in April, which suggests that the feeding activity of the fish was also highest in that month, the only other explanation being that the vulnerability of the food organisms was very much higher at the beginning of the season than subsequently. This latter possibility cannot be tested from the data, but from the discussion of §9.4.3.2.3 on the variation of intensity of feeding with 'hunger' it would be expected that the grazing mortality indices would decrease as the consumption of food increased. That such a trend occurred can be shown by plotting the grazing indices of Fig. 9.1 against Neill's indices (p. 508) of the average weight of the stomach contents in each month. The result for *Simulium* (larvae), *Simulium* (pupae) and Trichoptera is shown in Fig. 9.2, there being a reasonably well-defined trend in each case. The main features of Neill's observations seem therefore to be in harmony with our theoretical treatment of predation of a fish population on a mixed food supply of varying composition and abundance.

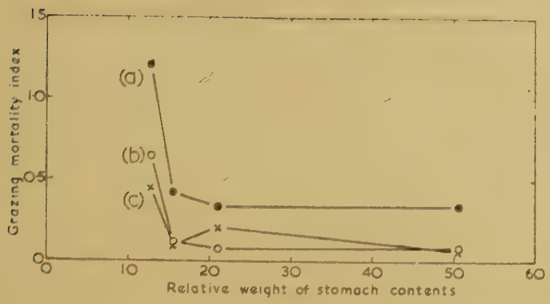

FIG. 9.2 GRAZING MORTALITY AND FOOD CONSUMPTION

[The grazing mortality indices shown in Fig. 9.1 for *Simulium* pupae (a), *Simulium* larvae (b) and Trichoptera larvae (c) are here plotted against the rate at which they were being consumed by trout, as estimated from stomach contents; data from Neill (1938) and Table 9.1. The decline of grazing mortality as the amount consumed increases suggests that the intensity of feeding decreased as the amount of food available increased.

Ivlev (1946) has investigated experimentally another aspect of this problem, namely the effect on the relative quantities of different foods consumed, of the way in which each is distributed in the feeding area, the relative amounts of the foods being kept constant. Ivlev showed that the indices of electivity for each food had greater variability when the degree of aggregation of all foods was increased by the same amount, though their mean values remained unchanged. If the degree of aggregation of one food only was increased, the index for this food changed. We are unable to ascertain whether these results indicate that changes occurred in the true preference for each food, but the increase in variability of the indices when the aggregation of all foods was increased suggests that at least part of the effect observed by Ivlev was due to a tendency for the fish themselves to aggregate on local concentrations of food. Over a short period of time (Ivlev's experiments were of 2 hours' duration) this would increase the number of contacts established by fish with the food that is distributed in this way and would result in an increased consumption of it without necessarily involving an increase in preference for that food. The interesting possibility raised by these experiments is that if, as is likely, fish tend to aggregate on local concentrations of food, a given fish population will exert a greater grazing mortality according to the degree of aggregation of food organisms. A similar problem will be discussed in detail in §10.2 with reference to the effect of aggregation of fishing vessels on the fishing mortality caused by them, and the relationship between the rate of dispersion of fish and the concentration of food organisms receives further mention in §10.2.4.

9.4.3.3 *The effect of aggregation of food organisms on the efficiency with which they are utilised by fish*

In the preceding section we mentioned the effects that the degree of aggregation of food organisms might have on the rate at which they are consumed by fish. Another aspect of this problem concerns the efficiency with which an aggregated food is utilized by fish, and is worth discussing briefly at this point.

From what has been said in §9.4.3.1.2 concerning the relationship between amount of food consumed and efficiency with which it is utilised, it would be expected that the amount of growth produced by an organism from a certain amount of food taken in over a given period would depend on whether it was ingested more or less continuously in small portions or in one or a few large meals. Gordon and Tribe (MS)* have shown that this effect was very marked when each member of a group of 22 sheep was fed with a constant daily ration, one batch of 11 being given one large feed per day and the remainder having eight daily feeds at hourly intervals. Over a nine week period the growth increment produced by the latter method of feeding was approximately five times that of the former. Similar effects of feeding frequency have been found by Palmer, Robinson and Burrows (1951) working with artificially reared fingerlings of the blueback salmon (*Oncorhynchus nerka*). Now, Sokolov and Chvaliova (1936) for *Gambusia affinis* and Allen (1941a) for salmon (*Salmo salar*) have shown that there are regular cycles of feeding, the stomach emptying with a definite periodicity. A similar phenomenon was found in plaice by Jones (1952); moreover, it must be that food is eliminated from the gut of this fish—which feeds only in daylight—in less than 24 hours, since they were usually empty or nearly so when caught early in the morning. This suggests that feeding in fish could reasonably be treated as a sequence of discrete meals, and a simple approach to this problem might be made by modifying Kostitzin's equation relating the gross and net assimilated energies.

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*The authors are indebted to Drs. J. G. Gordon and D. E. Tribe for their co-operation in making available their data from experiments on sheep feeding conducted at the Rowett Research Institute, Aberdeen.

If X denotes the gross amount of energy consumed as food during a given period in the course of n equal meals, each of which is fully digested before the next is taken in, the size of each meal is then X/n. Let the net energy obtained from any one of these meals be x_i; from Kostitzin's equation we then have

$$x_i = \frac{1}{k} \tanh \left(k\sigma \frac{X}{n} \right)$$

and the total net energy assimilated during the period is

$$x = nx_i = \frac{n}{k} \tanh \left(k\sigma \frac{X}{n} \right) \quad \ldots \quad \ldots \quad \ldots \quad (9.60)$$

If X is constant, the curve of x against n predicted by this equation is concave downwards, as is in fact required by the sheep data, and x tends to a limit of σX as $n \to \infty$. Clearly this equation cannot hold for very high values of n since the assumption that meals do not overlap would not be valid under these conditions. The real upper limit must be rather less than σX since this implies that the efficiency of utilisation has its maximum possible value $x/X = \sigma$, which could only be attained if each 'unit meal' was infinitely small.

In the absence of experimental data relating to fish species the treatment cannot be carried further here, but it is useful to point out the conditions under which this effect might be of some relevance in the assessment of the relationship between growth and density in fish populations. In the case of demersal fish feeding on populations of worms, molluscs, etc., the concept of a 'meal' which can vary in size has a meaning only if the organisms of the food population are not uniformly distributed but are aggregated to some extent and eaten in groups by fish. To take a simple case for purposes of illustration, we might envisage a population of food organisms distributed in local groups or 'clusters', each of which provides a 'unit meal' for a fish, and that n such clusters are present in the area that a fish can search during a given period of time. If now a change in the overall abundance of the food organisms involves a change in the number of individuals making up each cluster but not in the number of clusters per unit area, n of (9.60) will remain constant, and the efficiency of utilisation of the food organisms by fish will be given correctly by the methods of the previous sections. At the other extreme, however, it might be that a change in abundance of the food organisms took place by a corresponding change in the number of clusters per unit area but not in the number of individuals in each cluster. In this case the size of each 'unit meal' would remain constant, i.e. the ratio X/n of (9.60) would be constant, and the efficiency of utilisation would not vary. If the equations of the previous sections were applied to data of this kind, the effect would show itself as a direct variation of k with the degree of aggregation.

The way in which individuals of natural populations are distributed has received considerable attention in recent years, and the fact that the distributions are seldom uniform has led to the theoretical study of contagious distributions. Anscombe (1950), for example discusses the application of the negative binomial and logarithmic series, and other papers which may be cited in this connection are those by Cole (1946) and Williams (1947). The species so far studied do not include marine invertebrates, but from the results of benthos surveys such as those of Davis (1925) it would seem that there are likely to be marked differences between the density of food organisms in one major area and another. The aspect of the problem as it concerns marine benthos which does not yet seem to have been investigated and which the above discussion suggests might be of some importance when comparing the net productivity of two areas, is whether the non-uniformity of the distribution of food organisms extends to small distances so that they occur as 'clusters' which could result in fish having to obtain discrete meals.

9.4.3.4 *Destruction of food organisms by fishing gear*

To conclude this discussion of the dependence of growth on density and food supply, we return to the problem mentioned in §9.4.2, namely the possibility that some destruction of food organisms may be caused by the direct action of fishing gear. From what was said in that section in the case of trawl gear, it is reasonable to suppose that this effect would be the result of the trawl killing a certain *proportion* of the food organisms that lie in its path. To a first approximation we may therefore represent this 'destruction mortality' by means of a simple exponential coefficient which is proportional to the fishing mortality coefficient F. Thus denoting the constant of proportionality by $\varkappa$, we may restate (9.38), giving the annual food consumption of a population, in the form

$$\Xi = G \, . \, r\omega \int_{0}^{\lambda'} e^{-(G + \varkappa F)\psi} d\psi$$

$$= \frac{G \, . \, r\omega}{G + \varkappa F} \left(1 - e^{-(G + \varkappa F)\lambda'}\right) \quad .. \quad .. \quad .. \qquad (9.61)$$

This expression for Ξ can be used in place of (9.38) in the later equations of §9.4.3. Population models based on the methods of §9.4.3.2 with Ξ evaluated by means of (9.61) would take into account the destruction of fish food by fishing gear, and the resulting assessments would be modified according to whether or not the predicted changes in density of the population were due to changes in the amount of fishing or the selectivity of the gear.

Apart from direct experimental evidence on the destruction of bottom fauna by a trawl, an estimate of the constant $\varkappa$ could theoretically be obtained by comparing the growth-density relationships obtained on the one hand from data in which density changes were due to natural fluctuations in population numbers or to a change in gear selectivity, and on the other from data in which density changes were due to changes in fishing effort. As mentioned in §9.4.2 we should expect to find, if the destruction mortality was appreciable, that the growth-density relationship deduced from the latter kind of data was less pronounced than that from the former, and the required value of $\varkappa$ would be that which reconciled the two.

SECTION 10: SPATIAL VARIATION IN THE VALUES OF PARAMETERS: MOVEMENT OF FISH WITHIN THE EXPLOITED AREA

In all the foregoing discussion it has been assumed that parameters take equal numerical values over the whole of the exploited area. In no exploited fish population, however, will this condition be strictly satisfied, though in the case of certain factors such as growth it will usually be sufficient to use mean values of parameters weighted according to the density of fish in each 'growth area'. The degree of spatial variation in other factors, notably fishing intensity, may be great, and the main purpose of the following treatment is to set up population models which take such variation into account. Except in one special case discussed in §10.1, this will introduce a factor not previously considered, namely the movement of fish within the exploited area.*

10.1 The Case in which Movement is Strictly Localised

This situation is probably rare in major fisheries, though an approximation to it might be found in fisheries based on species restricting their distribution to a specific type of habitat which occurs only in isolated localities. From the theoretical point of view, the importance of this situation is that it is the limiting case of the problems to be considered in the remainder of §10 in which the movement of fish is taken into account.

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*As mentioned in §8.3.1, the yield from a fishery in which the fishing effort is uniformly distributed is independent of the distribution of the fish. The introduction of the movement of fish as a factor in population models does not therefore become relevant until the non-uniform distribution of fishing effort is taken into account also.

To introduce a terminology which will be used in the later parts of §10, we consider the exploited area as divided into a number of 'sub-areas' of sizes small enough for effectively uniform conditions to exist within each. If we designate the sub-areas with respect to two co-ordinates *u,v* and the corresponding parameter values by the same prefix, the yield from the sub-area *u,v* can be written as

$$ {}_{u,v}Y_W = {}_{u,v}F \int_{t_{\rho'}}^{t_\lambda} {}_{u,v}N_t \cdot {}_{u,v}w_t \, dt \quad \ldots \quad \ldots \quad \ldots \quad (10.1) $$

where

$$ {}_{u,v}N_t = {}_{u,v}R' e^{-({}_{u.v}F + {}_{u,v}M)t} $$

The yield from the whole area is therefore

$$ Y_W = \sum {}_{u,v}Y_W $$

so that with the values of the parameters known for each sub-area, a knowledge of any given distribution of fishing effort will enable an assessment of the total yield from the area to be made.

10.2 INTERCHANGE OF FISH BETWEEN ADJACENT SUB-AREAS

10.2.1 *The concept of random dispersion*

The migration patterns of fish populations have been the subject of numerous investigations and in a few cases they are known with some accuracy. For the most part, however, the emphasis has been on the direction and distance of well-marked population movements, such as spawning migrations. Underlying these clearly defined directional trends involving the population as a whole are the more local movements of individual fish which are responsible for the continual interchange of fish between adjacent areas within the general habitat, whether the population as a whole is moving or is static. The relative importance of directional migrations and local interchange varies greatly; in certain pelagic fish such as herring, the whole population is concentrated for much of the time into a relatively small part of its range and moves effectively as a unit. With demersal fish such as plaice, some individuals are usually to be found at any one moment throughout the range of the species, and although the distribution of the population may be markedly non-uniform such directional migrations as do occur are much more in the nature of shifts in the mean centres of population density. It is this latter kind of distribution with which we are primarily concerned, and in the following discussion we develop a theoretical treatment of population movement which is based on the local movements of individual fish, but we shall show that certain modifications can be introduced enabling phenomena such as shifts in the centres of density and even pronounced directional migrations to be incorporated within the same theoretical framework (§§10.2.3.2 and 10.2.5).

Relatively little seems to be known about the mechanism underlying local movements of fish from which we could deduce, for example, the extent of mixing between two groups of fish initially in adjacent areas of given sizes that would have occurred after any given interval of time. It is information of this kind, nevertheless, that is required in order to analyse problems involving the spatial distribution of fishing effort. Such evidence as is available concerning changes with time in the distribution of animals living in a relatively uniform environment (which, in the main, is characteristic of marine fish) indicates that there is often a random element in the local movements of individuals which is responsible for the movement of the population as a whole having properties similar to the phenomenon of physical diffusion of gases or of flow of heat in a conducting medium. For this similarity to hold it is not necessary that *every* movement should be haphazard or random in character, though the frequency of random movements is largely responsible for the time-scale on which the similarity will be observable. Thus Przibram (1913, 1918) has found that dispersion of a group of *Paramoecium* follows accurately the laws of physical diffusion if measured on a time-scale of minutes and a distance scale of millimetres,* but we should not expect this to be true for higher animals. At the other extreme Skellam (1951a) has shown that the spread of the muskrat (*Ondatra zibethica*) over distances up to 300 miles in central Europe follows the same laws with a time scale of years, but it is probable that movements of this population during periods of weeks or even months and over shorter distances could not be described as random. Intermediate cases are furnished by the work of Gilmour, Waterhouse and McIntyre (1946) on dispersion of the sheep blowfly (*Lucilia cuprina* Wied.), which followed the laws of diffusion when measured after two and a half days from the time of release, and over distances of one and two miles, and the studies of Dobzhansky and co-workers on dispersion in *Drosophila spp*. (see Burla *et al.*, 1950), which showed approximation to random dispersion when the distribution of flies was measured after periods of a few days from release and over distances up to hundreds of metres. In §15.1.2.1 we give an analysis of the spread of plaice from the nursery grounds on the eastern side of the North Sea, based on data of the distribution of certain year-classes over a range of about 80 miles at yearly intervals, which indicates that the basic mechanism of movement is, again, similar to diffusion.

From these observations it would seem that the concept of random diffusion might be a suitable basis for developing a theoretical treatment of movement of fish and dispersion of fish populations.† The mathematical techniques have been known for a long time and were developed by Maxwell in his classical studies on the kinetic theory of gases. Recently, a full discussion of the mathematical basis of random diffusion and its application to the dispersion of animal populations has been given by Skellam in the paper referred to above, and in what follows we need give only as much theory as is necessary for an interpretation of the concept in the case of fish populations.‡

In the kinetic theory of gases each particle is regarded as moving in a straight line until it collides with another, after which its movement is in a direction which is random with respect to that of its previous movement. We need not pursue this analogy rigorously in the case of fish, but in the first instance it is necessary to suppose that if we were to follow the movements of an individual fish we should find that after a certain interval of time its direction of movement would be unrelated to or, more precisely, could not be deterministically predicted from, that initially observed. For the dispersion of a group of such fish to follow the laws of diffusion, one criterion is that this time interval should be small relative to the time scale on which changes in the distribution of the group are measured. To give a specific example, we can imagine a bottom-living fish such as a plaice moving in a certain direction until it encounters a patch of food organisms, and after spending some time more or less stationary while feeding on these, continuing the search for food in a direction which is random with respect to that in which it first approached the patch of food organisms. In this case the 'inter-patch' movement would be analogous to the 'mean-free-path' in the kinetic theory of gases and would be the level at which the random direction component is introduced. We shall return to this question of the relation between movements of fish and abundance and distribution of their food in §10.2.4; for the moment it is sufficient to suppose that n movements in random directions are made in unit time and that the average distance covered by each is d. Then the effective 'velocity' of movement is

$$V = nd$$

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*This work is mentioned by D'Arcy Thompson (1948, p. 76) who discusses the phenomenon of random movement.

†Buchanan-Wollaston (1938) has discussed the possible application of the concept of random diffusion to a study of dispersal of fish, but gives no detailed treatment.

‡Useful accounts of the mathematics of heat flow and diffusion of gases are given by Margenau and Murphy (1948), and Carslaw and Jaeger (1948).

this velocity taking into account the time interval between each random movement. In all the following discussion we use the term 'velocity' in this sense, as defined by the above equation; an essentially similar definition is adopted by Leslie and Davis (1939) in their analysis of the process of random search and dispersion in a population of rats.

Now let us suppose that we observe a group of fish initially concentrated in a very small area which can be regarded effectively as a point in space. The partial differential equation defining the probability that any one fish will be at a point x, y measured from the origin of dispersion after time t is

$$\frac{\partial C}{\partial t} = \frac{1}{4}\frac{V^2}{n}\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right)$$

For the group of fish this equation defines the rate of change of concentration (density), denoted by C, with respect to time and distance, and the term V^2/n is analogous to the mean-square velocity in the kinetic theory of gases. If we let

$$\frac{V^2}{n} = D$$

then we have

$$\frac{\partial C}{\partial t} = \frac{D}{4}\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right) \qquad \ldots \quad \ldots \quad \ldots \qquad (10.2)$$

where D can be defined as the *dispersion coefficient*. It is important to note that we have the relationships

$$D = \frac{V^2}{n} = V\left(\frac{V}{n}\right) = Vd = nd^2$$

so that rate of dispersion is a function of both the velocity, V, of the fish, and the length, d, of the mean free path. Now in the diffusion of gases the free path is terminated solely by collision with another molecule, and hence the value of d depends on both the velocity of movement and the concentration (density) of the gas. Consequently, the dispersion coefficient, D, is also a function of concentration; if the concentration is decreased the value of D will increase owing to an increase in length of the mean free path. With marine fish of the type we are considering, on the other hand, it is unlikely that 'collision' with another fish of the same population is an appreciable factor determining the length of the mean free path. The process by which a fish changes the direction in which it is swimming may well be largely unrelated to any specific factor, and when this is not the case a more probable cause is contact with an object 'external' to the population—food in the example mentioned above—or perhaps a predator. Thus the mean free path, and hence the dispersion coefficient D, is likely to vary in magnitude in different parts of the habitat, but it seems reasonable to suppose that it is effectively independent of the density of the population in question unless this is very high. This being so, we can use (10.2) to define not only the dispersion of a particular group of fish within an area occupied by other fish of the same population at the same density, but also the dispersion of fish into an area initially devoid of any other fish of the same population. A further implication of assuming that velocity and mean free path are largely unrelated is that in a given set of conditions the value of D is directly proportional to the velocity of movement.

With some problems it is convenient to use (10.2) as the basic differential equation; this is the case with a type of marking experiment described in §14.1.2.4.3 in which marked fish are released at a 'point', and with the analysis of the off-shore dispersion of plaice referred to above and given in §15.1.2.1. However, when setting up a population model that takes into account the spatial distribution of fish and fishing effort we are not so much concerned with the density of fish at any point within the exploited area as with the general pattern of distribution of fish in relation to that of fishing effort. For this purpose it is essential that differences in the fishing mortality coefficient and in the rate of dispersion of fish in various parts of the exploited area should be incorporated in the theoretical model, since it is the interplay between these factors that is responsible for the observed distribution of fish. A further complication is that the entry of fish to the exploited phase of the population may, as in North Sea plaice, be restricted to one or two sections of the boundary of the exploited area. While it is possible to visualise a theoretical model based on the rigorous theory of random diffusion that represents such a situation, the indications are that it would be exceedingly complex and difficult to handle. Some kind of theoretical simplification is therefore required, taking the form of an approximation to the rigorous treatment of random diffusion that nevertheless gives a reasonably faithful representation of the effects of fish aggregation and non-uniform distribution of fishing effort. We suggest that this can be achieved by replacing the dispersion coefficient D by a *transport coefficient*, T, which defines the relative rate at which the number of fish in a specified area changes as the result of dispersion across the boundary of that area.* Thus the rate of decrease in number due to transport we shall write as

$${}_t\left(\frac{dN}{dt}\right) = -TN \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.3)$$

where N is the number of fish at time t in the area in question. Since this treatment is fundamental to the following theory, it is necessary to discuss its implications before proceeding.

Let us suppose we have a closed area divided into three sub-areas A, B and C of equal size, as shown in Fig. 10.1, and that initially these contain fish in different concentrations C_A, C_B and C_C respectively. We also suppose that the density in each sub-area is initially uniform but changes abruptly at the boundary between each, and that rate of movement in each sub-area is the same. At any subsequent time some degree of interchange (mixing) between these sub-areas will have occurred and the concentrations will have become say C'_A, C'_B and C'_C. In terms of the transport coefficient, the rate of change of concentration in the middle sub-area B can be written

$$\frac{dC'_B}{dt} = -T\left\{C'_B - \tfrac{1}{2}(C'_A + C'_C)\right\} \quad \ldots \quad \ldots \quad (10.4)$$

Since in this example we are supposing the area as a whole to be closed, we are concerned in effect with dispersion in one dimension only (i.e. longitudinally) and (10.4) is similar to the corresponding form taken by (10.2) in such a case; the term $C'_B - \frac{1}{2}(C'_A + C'_C)$ is in fact the finite-difference approximation to the term $-\partial^2C/\partial x^2$ of (10.2). Thus the transport coefficient T, although an instantaneous coefficient with respect to time, can be regarded as the finite-difference equivalent with respect to distance of the dispersion coefficient D, which is an instantaneous coefficient with respect to both time and distance.

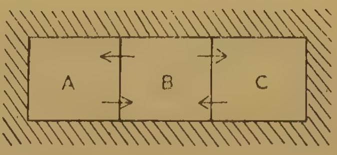

FIG. 10.1 REPRESENTATION OF INTERCHANGE BY MEANS OF TRANSPORT COEFFICIENTS

[Fish are assumed initially to be distributed uniformly but with a different density in each part A, B and C of a closed area. Their subsequent redistribution is formulated mathematically in the text to illustrate the use of transport coefficients as an approximate representation of random dispersion.]

It is seen from (10.3) that the use of transport coefficients implies that the rate of dispersal of fish from an area is proportional to the total number of fish in it, or in effect, to the average density of fish in the area. Strictly, however, this would be true only if the 'velocity' of fish within the area was infinite, so that the probability of a fish crossing the boundary in any short interval of time was constant. In reality, it is of course only the density of fish actually on the boundary that determines the rate at which fish are leaving the area,

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*Huntsman (1948) has distinguished *transportation* (passive movement) from *locomotion* (active movement). If we were to follow his terminology we should logically call T a coefficient of translocation since it refers to the resultant of active and passive movement, but as our use of the term 'transport' is unambiguous we have preferred to retain it because of its analogous use in physico-chemical theory.

and in general this will not be the same as the average density over the whole of the area. If, however, the boundary density is roughly constant ratio to the average density, then (10.3) will give the same representation of changes in average density as a result of dispersion as would be predicted by a rigorous treatment using the theory of random diffusion.* That a reasonably close approximation to this condition is likely to hold in practice can be shown by the following analysis, in connection with which we wish to acknowledge the assistance of our colleague Mr. J. A. Gulland.

Let us suppose that fish are contained within a rectangular area of length l, and that as in the previous example we are concerned only with longitudinal dispersion. In these circumstances the equation defining the density of fish at any given distance x from one end of the area after time t can be deduced from (10.2), and has the form

$$C_{x,t} = \sum_{n=1}^{\infty} k_n e^{-n^2\pi^2 t/Dl} \sin\frac{n\pi x}{l} \qquad \ldots \quad \ldots \quad \ldots \quad (10.5)$$

where $C_{x,t}$ is the density of fish at distance x after time t, and k_n is a constant determined by the initial distribution of fish, i.e. that at time $t = o$. Owing to the presence of n^2 in the exponent, the first term of the summation will decrease with t more slowly than any other term. Thus writing (10.5) for brevity in the form

$$C_{x,t} = \sum_{n=1}^{\infty} (C_{x,t})_n$$

we find, for example, that at a value of t such that the first term of the summation, i.e. $(C_{x,t})_1$, has fallen to half its initial value at $t = o$, subsequent terms have fallen to much smaller fractions of their initial values. The relationships are, in fact,

$$(C_{x,t})_1 = \frac{1}{2}(C_{x,0})_1$$

$$(C_{x,t})_2 = \frac{1}{16}(C_{x,0})_2$$

$$(C_{x,t})_3 = \frac{1}{512}(C_{x,0})_3$$

etc.

In addition, the particular form of the initial distribution may result in the first term of the summation having the greatest numerical value, as well as decreasing most slowly with time. For example, if the density is initially uniform in each half of the area but changes abruptly at the boundary, the constant k_n of (10.5) is zero for all even values of n and proportional to $1/n$ for all odd values of n. In this case, when the value of the first summation term has fallen to 0.5, the second and third terms have become

$$(C_{x,t})_2 = 0$$

$$(C_{x,t})_3 = \frac{1}{1536}$$

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*A good analogy is that of the cooling of a large object which is at a higher temperature than its surroundings. Unless the body is a perfect conductor there will be a temperature gradient within it (the outside being cooler than the inside), and an exact description of the rate of cooling would require analysis in terms of random diffusion (cf. 10.2)). A good approximation, however, is given by Newton's Law of Cooling, which states that the rate of loss of heat is proportional to the difference in temperature between the body and its surroundings (cf. (10.4)). It will be seen that the use of transport equations to describe the dispersion of fish from an area is a similar kind of approximation.

This analysis shows that for the greater part of the process of redistribution towards a steady state, the first summation term of (10.5) is by far the most important, and in many cases it is possible to write as a sufficient approximation

$$C_{x,t} \simeq k_1 e^{-\pi^2 t/Dl^2} \sin \frac{\pi x}{l}$$

From this expression it follows that the rate of change of density with time at any point can be approximated by a simple exponential function of time; hence the rate of change of the average density in, say, each half of the whole area can also be regarded as exponential with time. It will be appreciated that this is the property implicit in the transport equation (10.3).

These considerations indicate that a useful method of studying problems involving the spatial distribution of fish and fishing effort is to divide the whole area occupied by the fish population into as large a number of sub-areas as possible or convenient and to represent dispersion into and out of each sub-area by means of transport equations of the type (10.3). The size of sub-area should be as small as is consistent with the accuracy of commercial statistics of catch and effort, since the smaller the size the more faithful will be the representation obtained. The smallest practicable unit of area with British statistics of demersal catch and effort is the statistical rectangle, which in the Southern North Sea is roughly 30 by 30 miles. Taking this size of sub-area enables the area occupied by the plaice population to be divided into upwards of forty sub-areas, and is sufficient for most practical purposes (see also §10.2.3.1). The above example shows also that this method will be most satisfactory when used to predict steady state conditions, and most of the problems arising in practice are of this type.

The relation of the transport coefficient T to the basic parameters of movement of fish, such as velocity and number of movements per unit time, is similar to that of the dispersion coefficient D. For practical purposes the main difference between the two is that the value of T in a given case depends not only on the characteristics of movement of the fish, but also on the size and shape of the area to which it refers. To a first approximation, T is proportional to the perimeter/area ratio of the area, and this is sufficient when considering relatively small areas which do not differ too greatly in shape or size. If it should be necessary, however, to take into account the interchange between two large areas, it may not be satisfactory to compute a value of T for each from observed values referring to a much smaller area merely by adjusting according to the relative magnitudes of the perimeter/area ratios. The best procedure in such a case would be to construct a theoretical model with the large areas divided into sub-areas of the size to which the observed values of T refer. This would then be used either to solve the problem without dealing directly with the interchange between the large areas as such, or, in order to avoid excessive computation, to estimate an effective value of T for each large area so that subsequent analysis need deal with two or a few areas only.

We have discussed at some length the implications of using transport equations as a means of representing dispersion in fish populations in order to make clear that care is needed in their application owing to their approximate nature. Nevertheless, the indications at the present time are that neither knowledge of the mechanisms of dispersion nor accuracy of data and commercial statistics is sufficient to justify the labour involved in a rigorous treatment, and we suggest that the method enables working solutions to be obtained of a number of problems raised by spatial variations in fish density and fishing effort, that have not hitherto been attempted.

10.2.2 *A population model taking into account spatial variation in fishing intensity and movement of fish*

We can now return to an analysis of the situation outlined in §10.1 in which we suppose that the exploited area is divided into a number of sub-areas within each of which the values of all parameters can be taken as uniform, but here we allow for interchange of fish between adjacent sub-areas, the rate of dispersion being different in each. In view of the dimensional relationships of T, it is convenient to suppose that the sub-areas are of equal size and are square in shape; the differences between the values of T for the various sub-areas will therefore be due entirely to differences in the rate of movement.

Let us consider any one sub-area u,v and the four adjacent sub-areas $(u-1,v)$, $(u+1,v)$, $(u,v-1)$ and $(u,v+1)$, as shown in Fig. 10.2. Using transport coefficients the rate of change of number in the centre sub-area can be represented by the equation

$$\frac{d\,_{u,v}N}{dt} = -\left(_{u,v}F + {}_{u,v}M + {}_{u,v}T\right)_{u,v}N$$

$$+ {}_{u-1,v}\left(\frac{TN}{4}\right) + {}_{u+1,v}\left(\frac{TN}{4}\right) + {}_{u,v-1}\left(\frac{TN}{4}\right) + {}_{u,v+1}\left(\frac{TN}{4}\right) \quad .. \quad (10.6)$$

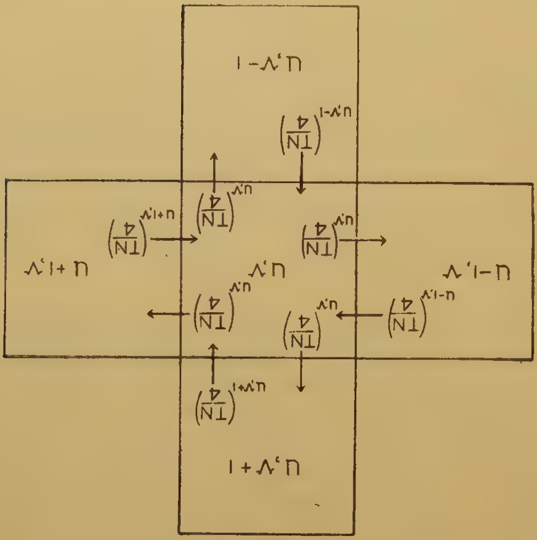

FIG. 10.2 DERIVATION OF (10.6) FOR INTERCHANGE BETWEEN ADJACENT SUB-AREAS

[This equation defines the rate of change of numbers of fish in the central square u , v in terms of the mortality rates there and interchange between it and the four adjacent squares.]

As an example of the integration of equations of this type we consider the case in which the water basin is divided into two sub-areas only, namely A and B. In this circumstance the only transport into or out of each sub-area takes place across the common boundary between the latter, and we have the pair of simultaneous equations

$$\frac{d\,_AN}{dt} = -\left(_AF + {}_AM + {}_AT\right)_AN + {}_BT\,_BN \quad .. \quad .. \quad (10.7)$$

and

$$\frac{d\,_BN}{dt} = -\left(_BF + {}_BM + {}_BT\right)_BN + {}_AT\,_AN \quad .. \quad .. \quad (10.8)$$

where $_AT$ and $_BT$ are the transport coefficients defined with reference to movement across the common boundary. These equations are a particular form of the generalised differential equations set up by Lanchester for the analysis of the strategical kinematics of warfare, and which are discussed in detail by Morse and Kimball (1951). They also correspond to von Bertalanffy's (1950b) system equations Nos. 8 and 9. This author gives the conditions for a steady state and a periodic solution, his equation No. 1 being analogous to our general transport equations. Using operator notation and solving simultaneously gives*

$$_AT\,_BT\,_AN = (D + {}_AF + {}_AM + {}_AT)(D + {}_BF + {}_BM + {}_BT)\,_AN$$

---

*The symbol D in the following equation is the operator, and is not to be confused with the dispersion coefficient denoted by the same symbol.

Putting ${}_AN = e^{mt}$ and differentiating gives a quadratic equation in m whose roots are

$$-\frac{1}{2}\left({}_AF + {}_AM + {}_AT + {}_BF + {}_BM + {}_BT\right)$$

$$\pm\sqrt{\left(\frac{{}_AF + {}_AM + {}_AT - {}_BF - {}_BM - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}$$

which we write as

$$-\alpha' \pm \beta$$

Therefore, on integration, we obtain

$${}_AN = e^{-\alpha' t}(Q\cosh\beta t + P\sinh\beta t)$$

where P and Q are constants of integration, which are found to be

$$Q = {}_AN_0$$

and

$$P = \frac{1}{2\beta}\left\{({}_BF + {}_BM + {}_BT - {}_AF - {}_AM - {}_AT)\,{}_AN_0 + 2\,{}_BT\,{}_BN_0\right\}$$

Substituting gives

$${}_AN = e^{-\frac{1}{2}({}_AF + {}_BF + {}_AM + {}_BM + {}_AT + {}_BT)t} \times$$

$$\times\Bigg[{}_AN_0\cosh\left\{\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}\right\}t +$$

$$+\frac{2\,{}_BT\,{}_BN_0 + ({}_BF - {}_AF + {}_BM - {}_AM + {}_BT - {}_AT)\,{}_AN_0}{2\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}} \times$$

$$\times\sinh\left\{\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}\right\}t\Bigg]$$

and similarly,

$${}_BN = e^{-\frac{1}{2}({}_AF + {}_BF + {}_AM + {}_BM + {}_AT + {}_BT)t} \times$$

$$\times\Bigg[{}_BN_0\cosh\left\{\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}\right\}t +$$

$$+\frac{2\,{}_AT\,{}_AN_0 + ({}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT)\,{}_BN_0}{2\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}} \times$$

$$\times\sinh\left\{\sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}\right\}t\Bigg]$$

Consequently, the annual yield in weight from each of the sub-areas, receiving ${}_AR'$ and ${}_BR'$ fish becoming liable to capture each year, and assuming that there is no difference in growth in each area, is given by,

$${}_AY_W = {}_AF\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{\alpha_n^2-\beta^2}\Big\{(\alpha_n\,{}_AR' + \beta\,{}_A\gamma)(1 - e^{-\alpha_n\lambda}\cosh\beta\lambda) -$$

$$-(\alpha_n\,{}_A\gamma + \beta\,{}_AR')\,e^{-\alpha_n\lambda}\sinh\beta\lambda\Big\}\quad \ldots\quad \ldots\quad \ldots\quad (10.9)$$

and

$${}_BY_W = {}_BF \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{\alpha_n^2-\beta^2} \Big\{ (\alpha_n\, {}_BR' + \beta\, {}_B\gamma)\,(1 - e^{-\alpha_n\lambda}\cosh\beta\lambda) - $$
$$- (\alpha_n\, {}_B\gamma + \beta\, {}_BR')\, e^{-\alpha_n\lambda}\sinh\beta\lambda \Big\} \quad \ldots \quad \ldots \quad \ldots \quad (10.10)$$

where

$$\alpha_n = \frac{1}{2}\left({}_AF + {}_BF + {}_AM + {}_BM + {}_AT + {}_BT\right) + nK$$

$$\beta = \sqrt{\left(\frac{{}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT}{2}\right)^2 + {}_AT\,{}_BT}$$

$${}_A\gamma = \frac{1}{2\beta}\Big\{({}_BF - {}_AF + {}_BM - {}_AM + {}_BT - {}_AT)\,{}_AR' + 2\,{}_BT\,{}_BR'\Big\}$$

$${}_B\gamma = \frac{1}{2\beta}\Big\{({}_AF - {}_BF + {}_AM - {}_BM + {}_AT - {}_BT)\,{}_BR' + 2\,{}_AT\,{}_AR'\Big\}$$

Equations of this kind have a direct application to assessment of the behaviour of a fish population in which there is no great spatial variation in growth but which is exploited by two independent fleets whose activities are confined to different parts of the area. In this case the two sub-areas are defined by the distribution of the fishing activity of the respective fleets, and (10.9) and (10.10) provide a means of assessing the yield obtained by each fleet in terms of the fishing intensity exerted by it and by the other fleet, and by the degree of interchange of fish across the boundary between the two sub-areas. A case of special importance is that of only part of the area occupied by the population being fished, but with interchange of fish between this and the unfished area. If the fished and unfished areas are each continuous and have a single common boundary, the yield could be assessed by means of the above methods, putting say ${}_BF$ to zero for the unfished area. More generally, however, the unfished part will not be continuous but consist of a number of separate areas, within the main exploited area, in which there is no fishing but which nevertheless contain fish that mix with those in the fished part; this is the case in the North Sea plaice, for example. An exact theoretical analysis of such a situation is complex and would probably be unsuitable for application, but an approximate treatment can be developed from the above theory along the following lines.

We consider a water basin of total area (A + B), where A denotes the total area fished and B the total area unfished, so that ${}_BF =$ zero. Also, the total unfished area B consists of smaller areas B_1, B_2, . . . B_r, . . . B_n, all contained within the fished area A. Movement of fish out of area A can therefore be only *into* one of the unfished areas, and must take place across the total perimeter length ${}_BP$ bounding all the B areas. Thus we have the relationships

$${}_BP = \sum_{r=1}^{n} {}_Bp_r = {}_AP \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.11)$$

where ${}_Bp_1$, ${}_Bp_2$, . . . ${}_Bp_r$ . . . ${}_Bp_n$, denote the perimeters of the areas B_1, B_2 . . . etc., and ${}_AP$ is the total perimeter length of all those boundaries of area A across which transport of fish can occur (i.e. other than the edge of the water basin itself). We denote by ${}_AT$ the transport coefficient referring to area A, and by ${}_BT_r$ that referring to the transport of fish from area B_r into area A. Now we mentioned in §10.2.1 that T is approximately proportional to the perimeter/area ratio of the area to which it refers; if we suppose for the moment that the rate of dispersion is the same throughout the area (A + B), then ${}_BT_r$ will differ from ${}_AT$ only by virtue of the relative dimensions of the areas B_r and A, and in fact we can write

$$ {}_BT_r = \frac{{}_AT\,A\,{}_Bp_r}{B_r\,{}_AP} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.12) $$

We may now consider the differential equations referring to the rate of decrease in number of fish in area A and in the total area B; taking M as the same in both areas we have

$$ \frac{d\,{}_AN}{dt} = -({}_AF + M + {}_AT){}_AN + \sum_{=1}^{n} {}_BT_r\,{}_BN_r \qquad \ldots \quad \ldots \quad (10.13) $$

and

$$ \frac{d\,{}_BN}{dt} = \sum_{r=1}^{n} \frac{d\,{}_BN_r}{dt} = \sum_{r=1}^{n} -(M + {}_BT_r)\,{}_BN_r + \frac{{}_Bp_r\,{}_AT\,{}_AN}{\sum\limits_{r=1}^{n} {}_Bp_r} \qquad \ldots \quad (10.14) $$

Substituting (10.11) and (10.12) in (10.13) and (10.14) we have

$$ \frac{d\,{}_AN}{dt} = -({}_AF + M + {}_AT){}_AN + \frac{{}_AT\,A}{{}_AP} \sum_{r=1}^{n} \frac{{}_Bp_r\,{}_BN_r}{B_r} \qquad \ldots \quad (10.15) $$

and

$$ \frac{d\,{}_BN}{dt} = -M\,{}_BN - \frac{{}_AT}{{}_AP}\left(A \sum_{r=1}^{n} \frac{{}_Bp_r\,{}_BN_r}{B_r} - {}_AN \sum_{r=1}^{n} {}_Bp_r\right) \qquad \ldots \quad \ldots \quad (10.16) $$

No general solution of these equations can be obtained owing to the presence of the summation term common to both, but certain particular solutions can be found which will satisfy most practical requirements.

(i) If, at any instant, the *density* of fish in each of the B areas is the same we have

$$ \frac{{}_BN_1}{B_1} = \frac{{}_BN_2}{B_2} = \ldots \text{etc.} \ldots = \frac{{}_BN_r}{B_r} \ldots = \frac{{}_BN}{B} $$

and substituting in (10.15) and (10.16) gives

$$ \begin{aligned} \frac{d\,{}_AN}{dt} &= -({}_AF + M + {}_AT)\,{}_AN + \frac{{}_AT\,A\,{}_BN}{{}_AP\,B} \sum_{r=1}^{n} {}_Bp_r \\ &= -({}_AF + M + {}_AT)\,{}_AN + {}_AT\,{}_BN\,\frac{A}{B} \qquad \ldots \quad \ldots \quad (10.17) \end{aligned} $$

and

$$ \frac{d\,{}_BN}{dt} = -\left(M + {}_AT\,\frac{A}{B}\right){}_BN + {}_AT\,{}_AN \qquad \ldots \quad \ldots \quad (10.18) $$

An approximation to this case may be found in populations in a steady state, in which there is roughly equal recruitment to each of the B areas. Assuming recruitment to occur during a relatively short period each year, the density in each of the B areas will oscillate about similar mean values.

(i) Similarly, if the perimeter/area ratios of all the B areas are the same, we have

$$ \frac{{}_Bp_1}{B_1} = \frac{{}_Bp_2}{B_2} = \ldots \text{etc.} \ldots = \frac{{}_Bp_r}{B_r} = \frac{{}_BP}{B} = \frac{{}_AP}{B} $$

so that again

$$ \sum_{r=1}^{n} \frac{{}_Bp_r\,{}_BN_r}{B_r} = \frac{{}_AP\,{}_BN}{B} $$

and we obtain (10.17) and (10.18) as before.

It will be seen that (10.17) and (10.18) are virtually identical to the simple two-area equations (10.7) and (10.8) and can be solved in a similar way. Thus in either of the above two circumstances we do not need to consider the number of the B areas or their separate sizes but only the magnitude of the total unfished area relative to that of A.

Equations (10.17) and (10.18) can give an approximation to the majority of cases met with in practice, especially for populations in a steady state. Such situations include that where a relatively large number of roughly equal B areas are of various shapes, or one B area is much larger than the remainder. The above methods are least satisfactory when there are two unfished areas of similar size but very dissimilar shape in which the densities are very different, or when there are a number of them which can be grouped on the basis of shape or density into two sharply defined categories having roughly the same total area. It may then be necessary to proceed as follows.

Let us suppose that the unfished areas fall into two groups which differ considerably in density or shape. Since the following discussion is concerned only with the B areas we can drop the prefixes and denote the perimeter, area and number of fish by p_1, B_1, N_1 and p_2, B_2, N_2 for the two groups respectively. In order to use the two-area equations (10.17) and (10.18), we need to express the summation term referred to above in the form

$$\frac{p_1 N_1}{B_1} + \frac{p_2 N_2}{B_2} = \alpha \left(N_1 + N_2\right) \left(\frac{p_1 + p_2}{B_1 + B_2}\right) \qquad \ldots \quad \ldots \quad (10.19)$$

where α is a constant if N_1 and N_2 are constant.

If we put

$$N_1 = kN_2$$
$$B_1 = lB_2$$
$$p_1 = mp_2$$

then (10.19) can be written

$$\left(1 + \frac{mk}{l}\right) \frac{p_2 N_2}{B_2} = \alpha \left(N_1 + N_2\right) \left(\frac{p_1 + p_2}{B_1 + B_2}\right) = \alpha \left(1 + k\right) \left(\frac{1 + m}{1 + l}\right) \frac{p_2 N_2}{B_2}$$

from which

$$\alpha = \frac{\left(1 + \frac{mk}{l}\right)\left(1 + l\right)}{\left(1 + k\right)\left(1 + m\right)} \qquad \ldots \quad \ldots \quad \ldots \quad (10.20)$$

If k, l and m are known, then α can be determined from (10.20), and we have

$$\sum_{r=1}^{n} \frac{{}_Bp_r\, {}_BN_r}{B_r} = \frac{\alpha\, {}_AP\, {}_BN}{B}$$

so that solutions of (10.17) and (10.18) can be obtained as before. If only two of the three constants k, l and m are known, limiting values of α can be obtained. If k, for example, is unknown then:

$$\underset{k=0}{\alpha} = \frac{1 + l}{1 + m}$$

$$\underset{k=1}{\alpha} = \left(\frac{l + m}{2l}\right) \left(\frac{1 + l}{1 + m}\right)$$

$$\underset{k=\infty}{\alpha} = \frac{m}{l} \left(\frac{1 + l}{1 + m}\right)$$

which can be inserted in turn in (10.17) and (10.18) to give the limiting solutions. It will be noted that because k, and hence α, are functions of N_1 and N_2, and thus of time, they are not strictly constants; but in a steady population k will oscillate about a constant mean value, so that they can be regarded as constants for practical purposes.

In the foregoing discussion we have taken the rate of dispersion as equal in both the A and B areas. We have not been able to obtain simple approximations when it is different in each of the B areas, but the important case of it being the same in all the B areas but differing from that in area A can readily be dealt with, and we use this case to show the form taken by the solutions of (10.17) and (10.18). If it is supposed that the velocity in the B areas is y times that in area A, then we have approximately

$$ {}_BT = y\,{}_AT\frac{A}{B} $$

Putting also, for brevity,

$$ \frac{A}{B} = z $$

equations (10.15) and (10.16) become

$$ \frac{d\,{}_AN}{dt} = -\left({}_AF + M + {}_AT\right){}_AN + y\,z\,.\,{}_AT\,{}_BN \quad .. \qquad .. \quad (10.21) $$

and

$$ \frac{d\,{}_BN}{dt} = \left(M + y\,z\,.\,{}_AT\right){}_BN + {}_AT\,{}_AN \quad .. \qquad .. \qquad .. \quad (10.22) $$

The annual yield in weight from the exploited area as a whole (i.e. in effect from area A) can be obtained by making the appropriate substitutions in (10.9), thus

$$ Y_W = FW_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'} - t_0)}}{\alpha_n^{\,2} - \beta^2} \Big\{ \left(\alpha_n\,{}_AR' + \beta\gamma\right)\left(1 - e^{-\alpha_n\lambda}\cosh\beta\lambda\right) $$
$$ - \left(\alpha_n\gamma + \beta\,{}_AR'\right)e^{-\alpha_n\lambda}\sinh\beta\lambda \Big\} \quad .. \qquad .. \quad (10.23) $$

where $F \equiv {}_AF$, and is proportional to the fishing intensity in area A, and also

$$ \alpha_n = \frac{1}{2}\Big\{F + {}_AT\,(1 + yz)\Big\} + M + nk $$

$$ \beta = \sqrt{\left\{\frac{F + {}_AT\,(1 - yz)}{2}\right\}^2 + yz\,{}_AT^2} $$

$$ \gamma = \frac{1}{2\beta}\Big[{}_AT\Big\{yz({}_AR' + 2{}_BR') - {}_AR\Big\} - F{}_AR\Big] $$

The properties of (10.23) are illustrated in §18.7, but we may indicate here the kind of problems of which some appreciation can be obtained by means of this model. Its main characteristic is that it takes some account of *cover*, this term being used here in an ecological sense and synonymous with *refuge* (Elton, 1939), i.e. that part of the habitat of the prey into which the predator cannot penetrate. A classic example of such a situation is the experimental predator-prey system of *Paramoecium* and *Didinium* set up by Gause (1934), in which the addition of a small amount of sediment to the culture provided sufficient cover for the *Paramoecia* for their extermination by the *Didinium* population to become impossible. Huntsman (1948) states that under natural conditions turbidity of the water is a significant factor modifying the mortality of salmon by predation, and according to Hartley (1947), Deelder (1951), Ball (1952) and others, the density of rooted plants in freshwater is often a limiting factor for the availability of food organisms (insects, molluscs and other fish, etc., as the case may be) to fish populations. Partial protection of these kinds could be assessed by similar methods.

In the case of a demersal fishery, cover may consist of any rough ground unsuitable for trawling which nevertheless contains fish. Equation (10.23) can thus be used to evaluate the yield under such circumstances, and hence to predict the effects of improvements in gear which enable fishing to take place on ground previously unfishable. Another example of the application of (10.23) is to the case in which part of the area inhabited by the population is beyond the range of the fishing vessels. This is the situation in the California sardine fishery, and has given rise to investigation of 'availability', i.e. the accessibility of the fish to fishermen (Marr, 1950). Another case is furnished by the Pacific Dover Sole (*Microstomus pacificus*), which has a great bathymetric range, and undergoes a seasonal spawning migration into water too deep for trawling, thus being protected from excessive depletion (Hagerman, 1952). Other uses of (10.23) are discussed in §18.7, including assessment of the value of closing areas to fishing as a regulative measure.

We supposed above that the fishing mortality coefficient in part of the area occupied by the fish population was zero. Solutions can be obtained in a similar way if the value of ${}_BF$ is finite but different from that in the remainder of the area, and these can take account of cover in the sense of conditions which hinder the predator, i.e. reduce the efficiency of the gear without excluding its use altogether. In the most general case, we have an exploited area which can be divided into a number of sub-areas with the fishing mortality coefficient differing in each, whether as the result of a varying gear efficiency or of different fishing intensities. The full analysis of this situation could be based on a family of equations of the type of (10.4), though no general solution can be given. Problems of a similar kind arise in other fields, however, and there are mathematical techniques for solving a family of simultaneous differential equations. Thus a useful analogy might be the methods used in the analysis of electrical networks (see Farrington, 1951), one type of which is known as the relaxation method (Southwell, 1946) and has already been applied to population problems by Riley, Stommel and Bumpus (1949). Finally, we would mention a conclusion of some importance which emerges from the above discussion, namely that there is no fundamental difference between the case in which only part of a population is fished at any one moment owing to the restricted range of vessels or the specialised requirements of the gear, and that in which the fishing effort is deliberately concentrated in those parts of the area where the population density is greatest, and each can be analysed by an appropriate form of (10.4). Moreover, in neither case does the average catch per unit effort provide a reliable measure of abundance, and this is the problem to be discussed in the following section.

10.2.3 *The concept of an effective overall fishing mortality coefficient*, $\tilde{F}$

10.2.3.1 *Evaluation of* $\tilde{F}$ *from past data*

So far we have been concerned with developing models by means of which it would be possible to *predict* the yield corresponding to any given distribution of fishing effort. These require a knowledge of the rate of dispersion of fish and of the spatial variation of this rate, but certain important relationships can be deduced in connection with the analysis of past data for which this information is not necessary.

One of the consequences of an unevenly distributed fishing effort is that there is no longer a simple relationship between fishing mortality and the total effort, but as we mentioned in §8.3.1 a useful approach in this case is to define an *effective overall fishing intensity*, $\tilde{f}$, which, if uniform over the area, would cause the same total fishing mortality as that actually observed. The latter can similarly be defined by an *effective overall fishing mortality coefficient*, $\tilde{F}$, and the relationship between $\tilde{f}$ and $\tilde{F}$ is independent of the relative distribution of fish and effort. We now show how $\tilde{F}$ and $\tilde{f}$ can be evaluated from a knowledge of the distribution of catch and effort.*

With the same teminology as in §10.2.2 we have immediately that the overall rate of decrease in number of the whole population is given by

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*We are indebted to Dr. P. H. Thomas for assistance with the following theorem.

$$\frac{dN}{dt} = \sum \frac{d\,{}_{u,v}N}{dt}$$

but

$$\sum \frac{d\,{}_{u,v}N}{dt} = -\sum ({}_{u,v}F_t + {}_{u,v}M_t)\,{}_{u,v}N_t \quad \ldots \quad \ldots \quad \ldots \quad (10.24)$$

since the sum of all terms containing T (see (10.6)) is zero in a closed population. Hence the rate of capture of fish in the sub-area u,v is given by

$$\frac{d\,{}_{u,v}Y_N}{dt} = {}_{u,v}F_t\;{}_{u,v}N_t$$

and the yield in numbers over a period of time τ by

$${}_{u,v}Y_{N,\tau} = \int_0^\tau {}_{u,v}F_t\;{}_{u,v}N_t\,dt \quad \ldots \quad \ldots \quad \ldots \quad (10.25)$$

Provided there are no great changes in the degree of aggregation of vessels or fish during the period τ, we can make the approximation of putting ${}_{u,v}F_t$ = constant = ${}_{u,v}F_\tau$ for the period τ. From (10.25) we therefore have

$$\frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau} = \int_0^\tau {}_{u,v}N_t\,dt$$

and summing both sides over all sub-areas gives

$$\sum \frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau} = \sum \int_0^\tau {}_{u,v}N_t\,dt = \int_0^\tau N_t\,dt \quad \ldots \quad \ldots \quad (10.26)$$

Now if we define an effective overall fishing mortality coefficient $\tilde{F}_\tau$ for the period τ, as the ratio of the total catch to the mean number present for all areas, i.e.

$$\tilde{F}_\tau = \frac{Y_{N,\tau}}{\int_0^\tau N_t\,dt} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.27)$$

the value of $\tilde{F}_\tau$ in a given case will produce the same total decrease in numbers and the same total yield in numbers over the period τ as that actually observed. Hence from (10.26) and (10.27) we have

$$\tilde{F}_\tau = \frac{Y_{N,\tau}}{\sum \frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau}} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.28)$$

The effective overall fishing mortality coefficient, $\tilde{F}_\tau$, is thus seen to be given by the ratio of the total yield in numbers to the sum of the catches per unit fishing mortality in the constituent sub-areas during the period. Furthermore, we may write (10.28) in the form

$$\tilde{F}_\tau = \frac{\sum {}_{u,v}F_\tau \frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau}}{\sum \frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau}}$$

But

$$\frac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}F_\tau} \propto {}_{u,v}\bar{P}_{N,\tau}$$

so that $\tilde{F}_\tau$ is the weighted mean of the fishing mortalities in the constituent sub-areas, the weighting coefficients being proportional to the respective mean numbers (or number-densities if the areas are unequal). Finally, since we have the relationship

$${}_{u,v}F_\tau = c \; {}_{u,v}f_\tau$$

where ${}_{u,v}f_\tau$ is the fishing intensity in the sub-area u,v during the period τ, the effective overall fishing intensity, $\tilde{f}_\tau$ is given as

$$\tilde{f}_\tau = \frac{1}{c}\tilde{F}_\tau \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.29)$$

From (10.27), (10.28) and (10.29) we therefore have

$$\tilde{f}_\tau = \frac{Y_{N,\tau}}{\sum \dfrac{{}_{u,v}Y_{N,\tau}}{{}_{u,v}f_\tau}} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.30)$$

It will be seen that the validity of these expressions for $\tilde{F}_\tau$ and $\tilde{f}_\tau$ does not depend on that of the assumption of random movement, since whatever form is taken by the transport terms of the set of equations of type (10.4) the sum of them for a closed population must be zero.

In those fisheries where fishing activity continues throughout the year, even though there may be some seasonal variation in its magnitude and distribution, it will usually be sufficient to take $\tau = 1$ year, and thus obtain by means of (10.30) an annual value of the effective overall intensity $\tilde{f}$ which will be weighted approximately according to the magnitude of the yield that has resulted from each of the various levels of fishing intensity existing during the year. Where seasonal variations in the magnitude of the fishing effort or its distribution relative to that of the fish population are too large to be smoothed in this way, it would be necessary to take values of τ less than one year, and choose them so that the year is divided into an appropriate number of time intervals within each of which it is reasonable to put $\tilde{F}_\tau$ constant. In this way we should obtain an estimate of $\tilde{f}_\tau$ (and hence of $\tilde{F}_\tau$) for each interval, which could be used in equations in which seasonal variations in the fishing mortality coefficient are taken into account.

It can therefore be seen that if we have data of fishing intensity and yield in each sub-area, either over periods of a year or, if necessary, for shorter time intervals, it is possible by the above methods to compute a value of the effective overall fishing intensity which, for vessels and gear of a given efficiency, bears a constant proportional relationship to a corresponding effective overall mortality coefficient. The latter is of more than theoretical interest, since it is this parameter that would be estimated from random age-composition samples of the commercial catch. Thus whenever it is necessary to compare mortality and intensity from past data, as in the methods of §14.3, it is desirable that the intensity should be computed in the way discussed above, especially if the fishery is one in which the spatial variation in fishing effort is large and changeable.

Another important application of the above methods is to the determination of an *index of total abundance* for the case in which the distribution of fish and fishing effort is not uniform—a problem which we have encountered on several previous occasions, notably in §8.3.1. In these circumstances the ratio of total catch to total effort does not give the index required, since the relationship between these two quantities depends on how the latter is distributed with respect to the former. What is needed is a measure of fishing intensity which is always proportional to the mortality coefficient which it generates, and from the above discussion it will be seen that such a measure is provided by the effective overall intensity, $\tilde{f}$. Thus an index of total numerical abundance that takes into account the relative distribution of fish and fishing effort is the total catch per unit effective overall intensity which, from (10.28), is

$$\frac{Y_N}{\tilde{f}} = \sum \frac{{}_{u,v}Y_N}{{}_{u,v}f} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (10.31)$$

An index of the annual mean biomass of the exploited phase is given in a similar way using catch in weight instead of numbers. To obtain an index of total abundance in a non-uniformly fished area we must therefore divide the whole area into as many sub-areas as are necessary to obtain an effectively uniform density of fish in each, and sum the ratios of the catch to intensity in each. The phrase 'effectively uniform' is important, because the true density may be far from uniform even in the smallest area that it is practicable to consider. What matters is that the area should be small enough for the relative distribution of fish and fishing within it to be reasonably consistent and, in particular, not correlated with changes in total abundance of the population or total fishing effort. If part of the area containing fish is not fished, the density in it must nevertheless be measured directly or estimated and included in (10.31); this might be done by sample hauls with a research vessel, for example, or by any other method such as echo-sounding, provided these estimates can be adjusted to correspond with the index of density obtained from statistics of the commercial fishing activity.

10.2.3.2 *Future prediction of $\bar{F}$*

We have been concerned above with computing estimates of effective overall fishing intensities and mortality coefficients from past data; another aspect of the problem is the prediction of the change in either of these quantities which will result from a proposed change in the total fishing effort or in its spatial distribution.

A change in the magnitude of the total fishing effort would have an approximately proportional effect on $\bar{F}$, but the effect of a change in its spatial distribution would be more difficult to predict. For this latter purpose it would be necessary to predict the changes in the values of ${}_{u,v}Y_N$, and this would involve the use of complex equations containing transport coefficients, as previously shown. We can, however, distinguish two special cases having simple solutions between which the true answer must lie, these depending on the relative magnitude of the mortality and transport coefficients. Thus, if the mortality coefficients are much greater than the transport coefficients the abundance of fish in any area is determined largely by the former, and taking M to be the same in each sub-area we may write

$$\frac{d\,{}_{u,v}N}{dt} \simeq -({}_{u,v}F + M)\,{}_{u,v}N$$

and

$${}_{u,v}N \simeq {}_{u,v}N_0 e^{-({}_{u,v}F + M)t}$$

so that

$${}_{u,v}Y_N \simeq \frac{{}_{u,v}F\,{}_{u,v}R'}{{}_{u,v}F + M}\left(1 - e^{-({}_{u,v}F + M)\lambda}\right) \quad \ldots \quad \ldots \quad (10.32)$$

We may therefore calculate the value of ${}_{u,v}R'$ given values of ${}_{u,v}F_1$ and ${}_{u,v}Y_{N1}$, for an observed situation, and hence, given any other set of values, ${}_{u,v}F_2$, we may calculate ${}_{u,v}Y_{N2}$, and thus $\bar{F}_2$.

On the other hand if the transport coefficients are large and greater than the mortality coefficients they will be mainly responsible for determining the relative densities in each sub-area. Hence the distribution of each year-class rapidly approaches a steady state as its age increases, and as $(F + M) \rightarrow$ zero we have

$$\frac{d\,{}_{u,v}N}{dt} \rightarrow \text{zero}$$

Hence, from (10.7), with ${}_AF$, ${}_BF$, ${}_AM$ and ${}_BM$ small, we have

$$\frac{{}_AN}{{}_BN} \simeq \frac{{}_BT}{{}_AT}$$

Consequently, for the population as a whole, and with the exploited area divided into any number of sub-areas A, B, C, etc., we can put

$$ {}_AN : {}_BN : {}_CN : \ldots \text{ etc. as } \frac{1}{{}_AT} : \frac{1}{{}_BT} : \frac{1}{{}_CT} : \ldots \text{ etc.} $$

We have, therefore, in general,

$$ {}_AN = \frac{N}{{}_AT \sum \frac{1}{T}} \; ; \; {}_BN = \frac{N}{{}_BT \sum \frac{1}{T}} \; ; \text{ etc.} $$

but

$$ N = N_0 e^{-(\bar{F} + M)t} $$

and $N_0 = R'$ and is the total recruitment to the exploited area. Hence

$$ {}_AN = \frac{R' e^{-(\bar{F} + M)t}}{{}_AT \sum \frac{1}{T}} $$

and

$$ {}_AY_N = \frac{{}_AF \, R'}{(\bar{F} + M)_AT \sum \frac{1}{T}} \left(1 - e^{-(\bar{F} + M)\lambda}\right) \quad \ldots \quad \ldots \quad (10.33) $$

If we put

$$ \frac{1}{{}_AT \sum \frac{1}{T}} = {}_Aq \; ; \; \frac{1}{{}_BT \sum \frac{1}{T}} = {}_Bq \; ; \text{ etc.} $$

then substituting (10.33) in (10.28) gives

$$ \bar{F} = \frac{{}_Aq_AF + {}_Bq_BF + \ldots \text{ etc.}}{{}_Aq + {}_Bq + \ldots \text{ etc.}} $$

But

$$ {}_Aq + {}_Bq + {}_Cq + \ldots \text{ etc.} = 1 $$

so that

$$ \bar{F} = {}_Aq_AF + {}_Bq_BF + \ldots \text{ etc.} \quad \ldots \quad \ldots \quad \ldots \quad (10.34) $$

With data of catch and effort for each sub-area it is therefore possible to compute a value of $\bar{F}$ from (10.28) and hence, from equations of type (10.33), to obtain estimates of the parameters ${}_Aq$, ${}_Bq$ . . . etc. As a first approximation these could be taken as constants, whereupon (10.34) could be used to predict the value of $\bar{F}$ that would result from any specified redistribution of fishing effort. The values of q are, however, measures of the tendencies of fish to aggregate in the various sub-areas; if these are determined wholly or in part by the local abundance of food they cannot be expected to remain unchanged if there is a redistribution of effort, since the density of fish and hence their grazing on the food will also change. To develop the analysis further it is necessary to return to the fundamentals of the theory of random search, which is the subject of the following section.

10.2.4 *Variation of dispersion rate with food abundance—the analysis of aggregation*

The only elaboration of the simple random dispersion hypothesis that has been necessary so far has been the introduction of differences between the rates of dispersion in the various sub-areas. Here we attempt to show how such variations could arise through the search for food, and to deduce the kind of relationships that might be expected in various circumstances between the rate of dispersion and abundance of food. In what follows we refer primarily to the dispersion coefficient D, though for reasons given in §10.2.1 the transport coefficient T will change similarly.

It is clear that there are a number of complicating factors that must be neglected in an analysis of this kind, but we believe that the general conclusions are not thereby invalidated. Thus it seems that plaice, which are visual feeders, forage only in daylight—at least in shallow water (see Jones, 1952). The occurrence within a small area of differences between the fauna of various types of sea bottom, raises the possibility that search for food may be directed by reaction on the part of the fish to a correlated factor, such as the texture of the substrate. Laing (1937) has discussed similar and other complicating factors in his analysis of the search for hosts by parasites, and has concluded that search ceases to be random when the parasite (*a*) is attracted by the correlated qualities of a host-containing area, (*b*) searches that area systematically, (*c*) is in the area of perception of the host, or (*d*) moves away from one host in such a way as to increase its chance of meeting a neighbouring host. This list might apply also to fish as predators on benthic animals, but it would be expected that conditions (*a*), (*d*) and certainly (*c*) would, if present, be adequately accounted for by the use of transport coefficients, at least to a first approximation. If, however, it should be that a correlated factor such as type of substrate is the immediate stimulus, rather than the food itself, the tendency would be for the rate of dispersion in each area to be largely independent of the contemporary abundance of food; hence the parameters ${}_Aq$, ${}_Bq$ . . . etc. of (10.34) could reasonably be taken as constants and the simple method for predicting $\bar{F}$ outlined previously would hold good. Systematic search (condition (*b*) above) could be undertaken by animals only in an extremely varied environment or where there is some simple symmetry, such as the leaves of a plant, and is scarcely relevant to our present problem. On the whole, therefore, there would seem to be no serious objection to applying the theory of random search to the problem of the search by fish for their food.

While a fish is searching for food we might suppose that each random movement is the progression from one patch of food organisms to another; by defining the effective velocity as $V = nd$, n can now be regarded as the number of food patches visited by the fish per unit time and d as the average distance that has to be covered after leaving one patch until the next is encountered. It will be remembered that V takes into account any period during which fish are effectively 'at rest' while grazing on a food patch, but we now need to refer to this time specifically, and we denote it by t^0. Thus we can write (see §10.2.1)

$$\frac{1}{D} = \frac{1}{d}\left(\frac{t'}{d} + \frac{t^0}{d}\right)$$

where t' is the average time taken by fish to swim from one food patch to the next. If we denote the true swimming velocity by V' and regard this as constant, we have

$$\frac{1}{D} = \frac{1}{d}\left(\frac{1}{V'} + \frac{t^0}{d}\right) \qquad \text{.. .. .. ..} \quad (10.35)$$

We can now see from (10.35) the change in the value of D that can be expected to result from a change in the abundance of the food organisms.

(i) Suppose first that the latter involves a change in the number of food patches per unit area but that the size of each patch remains constant. In this case t^0 is constant but d will vary inversely with the total biomass of the food organisms, and with the terminology of §9.4.3.2.4 we can put

$$d \propto \frac{1}{\bar{p}w}$$

We may now distinguish two cases, according to whether the time spent feeding is much larger or much smaller than the time taken to swim from one food patch to the next. Thus if $t^0 \gg t'$, i.e. $1/V' \ll t^0/d$, we find from (10.35) that

$$\frac{1}{D} \simeq \frac{t^0}{d^2} \propto \bar{p}^2_W \quad \text{.. .. .. ..} \quad (10.36)$$

whereas if $1/V' \gg t^0/d$ we have

$$\frac{1}{D} \simeq \frac{1}{dV'} \propto \bar{p}_W \quad \text{.. .. .. ..} \quad (10.37)$$

(ii) At the other extreme we can suppose that a change in total biomass of the food organisms is the result of a change in the size only of each patch, the number of patches per unit area remaining constant. In this case d will be constant but t^0 will vary roughly as the size of the patch, i.e. we can put

$$t^0 \propto \bar{p}_W$$

Then if $1/V' \ll t^0/d$, we have

$$\frac{1}{D} \simeq \frac{t^0}{d} \propto \bar{p}_W \quad \text{.. .. .. ..} \quad (10.38)$$

while if $1/V' \gg t^0/d$, we have

$$\frac{1}{D} \simeq \frac{1}{dV'} = \text{constant} \quad \text{.. .. .. ..} \quad (10.39)$$

From this analysis we find that if the time spent feeding (i.e. 'at rest') is large relative to the 'inter-patch' swimming time ((10.36) and (10.38)), the rate of dispersion is inversely proportional to a power of food abundance lying between one and two, according to whether changes in food abundance are the result primarily of changes in the number of food patches or the size of each. On the other hand, if the feeding behaviour is such that food is taken in whilst actively swimming—as in a plankton feeding fish, for example—the effect on the rate of dispersion is less pronounced; but with most cases of selective feeding, in which fish seize each food organism individually, an increase in food abundance will slow down the rate of dispersion to some extent as a result of decreasing the 'mean free path' (10.37). If feeding influences neither the resultant velocity nor the rate of change of direction D is, of course, independent of the abundance of food (10.39) but this could result only from a purely mechanical feeding behaviour that is not likely to be found in fish.*

The population model formulated in (10.6) can therefore represent the case in which the search for food is random with fish tending to aggregate in those areas where the density of food organisms is greatest. For example, if we assume that the coefficients $_Aq$, $_Bq$, etc. of (10.34) are constant it will imply that the distribution of food is not appreciably altered by any change in the distribution of fish that might result from a change in that of fishing effort. We can, however, take into account the effect of grazing on the local density of food by writing relations of the kind

$$\frac{1}{_AT\sum \frac{1}{T}} \propto {_A\bar{p}_W}^b \quad \text{.. .. .. ..} \quad (10.40)$$

where $_A\bar{p}_W$ is the standing crop of the food population in sub-area A, and the summation term takes into account changes in rate of movement that are not correlated with food supply. The value of the power b will depend on the mechanism of aggregation as

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*Thorpe (1951) gives a useful summary of terms suggested to describe situations such as those outlined above. He defines a *kinesis* as locomotory behaviour not involving a steering reaction but in which there may be turning, random in direction. In *orthokinesis* the rate of movement, and in *klinokinesis* the amount of turning, is related to the intensity of stimulation, which here is clearly a function of the food density. Taxes, which we meet in §10.2.5, he describes as spatial correction movements (or turning components) resulting in orientation.

discussed above but will probably not differ much from unity. By methods such as those developed in §9.4.3.2.3 we may express ${}_{A}\bar{p}_{W}$ in terms of the parameters of the food population and of the density of the fish population grazing it. In this way a population model could be constructed which takes account of factors tending to compensate for the effect of changes in distribution of fishing effort on that of the fish population. For example, it could represent the situation in which an increase in fishing intensity in a particular sub-area causes a decrease in density of fish and a consequent increase in the abundance of food which, in turn, leads to a greater tendency for fish to aggregate in that area.

10.2.5 *Oriented dispersion—a theoretical model of a spawning migration*

Although with the above hypothesis a change in distribution of fishing effort or in that of the food organisms would cause shifts in the centres of fish density, changes in rate of dispersion in certain parts of the area, however marked, cannot be responsible for the typical spawning migration. The complete, or nearly complete, absence of mature fish outside the spawning area at spawning time, and the time relations and consistency of spawning migrations, can be adequately represented in a theoretical model only by introducing a directional element into the simple hypothesis of random movement. In this connection it is interesting to find that Wilkinson (1952), in a paper referred to again at the end of this section, has concluded that the hypothesis of random search, appropriately modified by the introduction of certain directional influences, provides a satisfactory interpretation of the available data on the homing of wild birds.

In his review of fish migrations, Russell (1937) has pointed out that the first migration of many marine fish, including plaice and cod, to their spawning grounds cannot involve memory, as they were carried away from them while still in the egg stage. Thus the ability of salmon to 'home' to the tributary in which they were reared (but, significantly, not to that in which they were spawned, if these are differentiated experimentally), is not in itself sufficient explanation of the means whereby plaice find their way to their spawning grounds, remarkable though the faculty is. Of the various environmental factors that have been suggested as guiding mechanisms for spawning migrations of fish, the weight of evidence is in favour of water currents. Certainly, they are unique in the present context, since unlike temperature or salinity, for example, a current has a direction as well as an intensity and is, in this sense, a vector quantity. Thus taking as an orienting mechanism any factor that is not a vector quantity makes it necessary to suppose that fish could either detect and react to differences in intensity of that factor within the length and breadth of its body, or carry a mental picture of its recent movements and corresponding changes in intensity of the factor, and navigate accordingly. Tait (1952) has assembled evidence in support of the view that the actual spawning process is controlled principally by temperature and believes also that this is in some way concerned with the migration. It is, of course, quite possible that not only temperature but other factors such as type of bottom, play an important part during the actual spawning process. But the possibility of temperature having any appreciable orienting influence on the migration of the fish that spawn in the Southern Bight of the North Sea (including plaice) is apparently ruled out, if for no other reason, by the fact that over much of their distance the migration routes run parallel to the isotherms.

The present choice seems to be either to accept water currents as at least the major environmental factor acting as an orienting influence on spawning migrations, or to abandon the idea that any external factor is operative and to suppose that fish have a highly developed innate sense of direction and timing. This latter alternative is, in fact, what Verwey (1949) concluded must be the true explanation in certain cases where he could find no evidence of any known factors that could account for the consistency with which fish migrate to their particular spawning area. Theoretical studies such as those outlined in this section clearly cannot by the nature of the problem help to discriminate between these two approaches. Our purpose is to show that by postulating the existence of a residual current—possibly with a velocity that decreases in the direction of flow—and by making use of certain behaviour mechanisms that are known to be possessed by some fish, a theoretical model can be set up that reproduces all the essential features of a spawning migration and offers a method of testing the hypothesis experimentally.

Let us suppose that the effect of a current is to cause fish to orientate preferentially in a contranatant direction, that is, that a fish is more likely to be facing into than away from the current at any moment. The existence of preferential contranatant orientation means that the rate of dispersion of the population will be a function of direction, and if orientation is sufficiently marked and the velocity of the current not too great, the population as a whole will migrate 'upstream'. To simplify the problem we may restrict analysis to dispersion in one dimension only, i.e. with or against the current, since this will allow a theoretical model to be developed which has the essential features of a contranatant spawning migration. In terms of transport coefficients we can therefore define the dispersion of fish from sub-area v in a direction parallel to that of the current, i.e. downstream and upstream, by the equation

$$\frac{d\,{}_vN}{dt} = -({}_vF + {}_vM + {}_vT_A + {}_vT_B){}_vN + {}_{v-1}T_A \cdot {}_{v-1}N + {}_{v+1}T_B \cdot {}_{v+1}N \quad .. \quad (10.41)$$

where ${}_vT_A$ and ${}_vT_B$ denote the downstream and upstream transport coefficients respectively. With a sufficient degree of orientation and not too great a current velocity, we shall have ${}_vT_B > {}_vT_A$, so that a greater proportion of fish leaving the sub-area v will do so upstream than downstream. To develop (10.41) in an analytical form we need to express the velocity, V_r, of fish relative to the bottom in terms of their velocity relative to the water, V, their orientation and the current speed s.

Referring to Fig. 10.3, the assumption of random (i.e. unorientated) movement implies that a fish at any point 0 would, at any time, be equally likely to be swimming in any direction, and we may represent the probability distribution of direction by means of a full circle.* Now let us suppose that a current flowing through the area in the direction shown by the arrow would cause fish to become preferentially orientated in the opposite direction. The probability that a fish will, at any moment, be facing in a direction between $\theta - 1/2\, d\theta$ and $\theta + 1/2 d\theta$ can be denoted by the function ${}_sp_\theta\, d\theta$, where

$$\int_0^{2\pi} {}_sp_\theta\, d\theta = 1$$

and θ is measured from the current direction, so that when $\theta = o$ the fish are swimming directly against it. The prefix s denotes the fact that the degree of contranatant orientation, and hence the form of the function ${}_sp_\theta$, can be expected to vary with the current strength, s. Huntsman (1948) discusses the influence of current speed in the rheotaxis of salmon, and Davidson (1949) has investigated this experimentally. The latter author found that an increased stimulus (current speed) induced an increased response (faster swimming), and that the contranatant swimming speed of yearling lake salmon increased linearly with current speed in such a way that the speed of translocation remained constant. It would be expected, however, that the true relation between stimulus and response would be asymptotic—it clearly cannot be proportional or even linear except over a restricted range of low stimulus values.

An example of the probability density for a case in which there is some degree of contranatant orientation is shown by the dotted curve of Fig. 10.3. The distribution shown is actually one of a family of circular transformations of a normal curve, in this instance, with $\sigma = \pi/2$ radians. Preliminary analysis by one of us (S.J.H.) of photographs of flocks of birds and of the orientation of foraging ants suggests that this type of distribution may have some general significance. It arises if animals that are all initially facing in one direction make successive small deviations of a certain magnitude equally to the left or right (cf.

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*This orientation diagram is constructed so that the probability that at any instant a fish will be facing between any two stated directions is the fraction that the area of that sector is of the whole figure, it being convenient to make the latter unity.

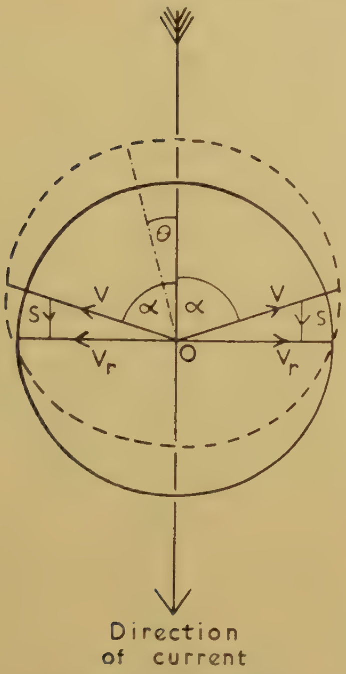

FIG. 10.3
PREFERENTIAL CONTRANATANT ORIENTATION

[A fish is assumed to be at point 0, influenced by a current flowing in the direction shown by the arrow. Its orientation probability is represented by the 'circles', the full circle being the case of no preferential contranatant reorientation and the broken figure (a circular transformation of a normal curve) showing some degree of preferential orientation.]

Skellam's (1951a) treatment of the one dimensional random-walk problem). Providing the current velocity is not greater than the velocity of the fish relative to the water, we can define a certain angle $\theta = \alpha$ such that a fish swimming in this direction would proceed relative to the bottom in a direction exactly at right angles to the current. This is shown in Fig. 10.3, and it will be seen that α is defined in terms of V and s by the equation

$$\cos \alpha = \frac{s}{V}$$

For the present purpose we need be concerned only with the *resultant* movement of fish relative to the bottom in a direction parallel to the current either upstream or downstream. Hence the probability that a fish is swimming in a direction such that its resultant movement is downstream can be written as

$$\int_{\alpha}^{2\pi - \alpha} {}_s p_\theta \, d\theta$$

and the probability that its resultant movement is upstream is

$$\int_{-\alpha}^{\alpha} {}_s p_\theta \, d\theta$$

The velocity of these resultant movements can also be defined. Thus a fish whose resultant movement is downstream must be swimming at an angle θ such that $\alpha < \theta < 2\pi - \alpha$, and its resultant velocity will be

$$(V_r)_A = - V \cos \theta + s$$

Similarly, for a fish moving upstream we have $- \alpha < \theta < \alpha$, and its resultant velocity will be

$$(V_r)_B = V \cos \theta - s$$

Hence the mean velocity of all fish moving downstream is

$$(\bar{V}_r)_A = \int_{\alpha}^{2\pi - \alpha} {}_s p_\theta \, (- V \cos \theta + s) d\theta$$

and the mean velocity of all fish moving upstream is

$$(\bar{V}_r)_B = \int_{-\alpha}^{\alpha} {}_sp_\theta\,(V \cos\theta - s)d\theta \quad \ldots \quad \ldots \quad \ldots \quad (10.42)$$

These mean velocities are related to ${}_vT_A$ and ${}_vT_B$ respectively of (10.41), but the particular form of the relationship depends partly on the mechanism of orientation. Thus the observation that the proportion of all fish which are facing upstream at a given moment is greater than that facing downstream could result from two different mechanisms; either the mean free path (relative to the water) is the same in all directions and preferential orientation occurs when the fish changes direction, or fish tend to swim for a longer time in a straight line when facing upstream than when facing downstream, i.e. the mean free path is greater in the contranatant direction. Each of these mechanisms or their combination would produce an essentially similar effect, though the above treatment is based on the assumption that the former is operative, i.e. with the mean free path constant in each direction. In this case $(\bar{V}_r)_A$ and $(\bar{V}_r)_B$ will be roughly proportional to ${}_vT_A$ and ${}_vT_B$ (see §10.2.1). In addition, it is possible that the actual swimming velocity upstream may be greater than that downstream, and if the mean free path is also greater in the upstream direction, the values of the transport coefficients will be more nearly proportional to the square of the resultant velocities. In practice we might expect to find a combination of all three possibilities, and the transport coefficients would probably be proportional to something between the resultant velocity and its square.

Although we are unable to define the precise relationship between the transport coefficients and the pattern of movement of the individual fish, the general features of the spawning migration predicted by the above model can be deduced. Thus during the feeding season we can suppose that the distribution of fish is determined largely by that of the food organisms, the reaction of fish to the current being sufficient merely to prevent them being swept downstream. With the cessation of feeding the tendency for fish to move upstream, by means of one or a combination of the above mechanisms, would become dominant, and if $(\bar{V}_r)_B > (\bar{V}_r)_A$ the centre of density of the population will move upstream. Relevant here is that Davidson (1949) has found experimentally that fish, swimming rapidly, translocated into fast water when not feeding; but when fed they fell back and aggregated in quieter water, though they still faced upstream. When the current was stopped they became disoriented. If we further suppose that the current velocity increases in the upstream direction, migration will continue until the centre of density reaches the point at which $(\bar{V}_r)_B = (\bar{V}_r)_A$, that is, at which dispersion is effectively the same both upstream and downstream. This point will become the centre of the stable distribution taken up by the population after migration is over; the form of the distribution, the position of the centre of density and the rate at which the stable distribution is approached, will depend on the details of the contranatant mechanism as discussed above, and the rate of change of current velocity with distance. For example, in the extreme case of perfect contranatant orientation, all fish will be facing directly against the current and all will, in theory, aggregate at the point where the current velocity is equal to their swimming velocity. More usually, orientation will never be complete, and the density of the spawning aggregation will decrease with distance from the centre of density in both directions, in which case the point at which $s = V$ will be the upstream limit of the distribution. Finally, we can suppose that spawning having occurred, the tendency to orientate contranatantly becomes negligible, so that $(\bar{V}_r)_B < (\bar{V}_r)_A$ and the spent fish are gradually carried downstream to the feeding grounds; at the same time they begin to disperse and their subsequent distribution again becomes determined primarily by the feeding stimulus.

A feature of this theoretical model of a spawning migration is the postulate that the current velocity increases in the upstream direction. This provides an automatic mechanism causing the population to aggregate for spawning at approximately the same place each year, irrespective of its distribution before the spawning migration begins. The timing of the actual spawning is therefore not critical, since the population will remain aggregated until the orienting reaction is weakened, i.e. until spawning has occurred. With a constant current velocity, on the other hand, it is necessary to suppose that the upstream migration is terminated by fish being aware of the location of the spawning ground or reacting to certain environmental features which are peculiar to it, or that fish cease migrating only when actual spawning begins, in which latter case it is not easy to see how an initially widely scattered population could aggregate in a relatively small spawning area.

A residual current exists in the Southern Bight of the North Sea, flowing north-eastwardly from the Straits of Dover with diminishing velocity, and the cycle of events postulated above does, in fact, represent the salient features of the feeding, spawning and recovery migrations of plaice and probably some other species of the Southern North Sea (Simpson, 1949). Indeed, a contranatant movement seems to be a remarkably general feature of spawning behaviour in fish, and Tait (1952) expresses the belief that the very few cases that appear at present to be exceptions to the contranatant rule may no longer be so when more detailed knowledge of the currents becomes available, as has happened in one instance already. On the other hand, the fact that a population would be unable to maintain itself in an area through which a current is flowing unless the spawning products were liberated a suitable distance upstream, means that evidence of this kind cannot provide positive proof of the role of currents. A more critical test is that described by Bowman (1933), in which plaice were taken from the East coast of Scotland to the Shetlands; the transplants on reaching maturity did not attempt to return to their ancestral spawning ground in the Moray Firth but instead joined in the contranatant spawning migration of the local Shetland stock. The conclusion from the above analysis is that a simple extension of the concept of random dispersion bringing in certain orienting effects of current, can lead to a theoretical model having the essential features of many spawning migrations, without it being necessary to postulate that fish are aware of the direction and distance of the spawning grounds.

It is interesting to find that the work of Wilkinson (1952) on the homing of wild birds has emphasized the importance, even when studying such apparently purposive phenomena as bird 'navigation', of giving due consideration to the type of model based on the hypothesis of random search that we have used above. This author has drawn the useful distinction between what he calls *anastrophic* migration, where animals move from one more or less well-defined area to another; and the *diasporic* kind, where in the non-breeding season the animals wander over wide stretches of territory, reassembling at the breeding stations in the following season. Most examples of fish migration would seem to be of the diasporic kind, and although Wilkinson's model of such a migration differs from ours in certain important respects, we believe these are due simply to fundamental differences between the environments of fish and birds. Thus a bird may have the sun to guide it, and can certainly recognise a particular locality; some other guiding factor must be postulated for fish, which we have taken to be current direction. It is also possible that 'position' indicators are necessary in fish migrations owing to the homogeneity of the habitat; we have shown above how current speed can operate in this way, but this does not preclude the possibility that fish may respond to other factors, such as type of bottom. It would seem that definite evidence for possible mechanisms of the spawning migration in fish such as plaice might come from experimental investigation of their reaction to currents. If definite contranatant orientation is observed and its degree in relation to current speed measured, the findings could be incorporated into a theoretical model such as that developed above to predict the time relations of the migration for comparison with that observed in practice. A similar approach has, in fact, been used by Evans (1951) to show how changes in the distribution and aggregation of chitons (*Lepidochitona cinereus* L.) under different tidal conditions can be interpreted in terms of the interaction of various taxes, including directional ones (geotaxes), and orthokinesis (the speed varying inversely as the light intensity).

10.3 Group Organisation of Fishing Units—The Problem of Fish Searching and the Concept of Optimum Fishing Tactics

We have hitherto been concerned with developing population models which give the fishing mortality, and hence the yield, resulting from a given total fishing effort distributed in a given manner over the exploited area, and we have found that in the general case this requires a knowledge of the movement patterns of the fish. Another type of problem arising from the spatial distribution of fishing effort concerns the relationship between a total effort of a given magnitude and the value of the effective overall fishing intensity, and hence the mortality that it will generate. This is obviously of great importance in fishery regulation, when having ascertained the most desirable fishing mortality it is then necessary to be able to predict the fishing effort required to produce it (see §19).

The process of which we must take account at this stage is *fish searching*, which when successful results in vessels tending to work most in those areas where the density of fish is greatest. The effects of this contagious distribution of fishing units are least important in those cases in which the fish are fairly uniformly distributed, or in which their occurrence in high concentrations is reasonably consistent with respect to time and place, and is known to the fishermen. These requirements may be satisfied in a number of fisheries, particularly demersal ones, and in such cases the effective overall intensity $\bar{\bar{f}}$ will be an approximately constant proportion of the average intensity $\bar{f}$ (and hence of the total effort) over a fairly wide range of population size, even though the two intensities may differ numerically. In other fisheries, of which those based on certain pelagic species provide the most obvious examples, the geographical distribution of the population is not only markedly non-uniform but the occurrence of high concentrations is to a greater or lesser extent capricious and unpredictable. In these circumstances we should expect that the searching power of the fleet, and hence the relationship between $\bar{\bar{f}}$ and $\bar{f}$, would be appreciably influenced by both the abundance of the fish population and the size of the fleet. A satisfactory solution to the problem of searching, allowing a prediction of the value of $\bar{\bar{f}}$ corresponding to any given value of $\bar{f}$ and total abundance of the fish population, would require a fuller discussion than we can give here, though we can indicate certain of the factors involved and a possible method.

The fact that the fishing mortality generated by a fishing fleet of a certain size depends partly on how the constituent vessels are distributed relative to the fish population, raises a number of important questions. The first point to note is that in each case, and for a given value of the total fishing effort, there is a certain distribution of the latter which would result in the maximum possible fishing mortality being generated. This we shall call the *limiting distribution of effort*, and it is achieved if the following two criteria are satisfied, namely:

(a) All vessels must be fishing at any moment on the same density of fish, i.e. the density must be the same in all parts of the fished area, although the latter need not be continuous.

(b) No part of the unfished area may have a higher density of fish than the fished area. In practice, these would imply that the fishing intensity is most concentrated where the fish themselves show the greatest tendency to aggregate. The limiting distribution of effort depends on the spatial variation of the rate of dispersion of the fish, and might very well be extremely irregular in form and have pronounced maxima. It is interesting and important to note in this connection that a distribution closely approximating to the limiting distribution is taken up by the British trawler fleet in one of the most heavily fished parts of the Southern North Sea, since we have found that certain areas in which the tendency of fish to aggregate is very different are nevertheless trawled in such a way that the density of fish is kept about the same in all of them (see §14.1.3.3).

To develop the argument further, let us first suppose that the aggregating tendencies of fish remain constant so that the centres of density of the population remain stationary, and consider the searching tactics that the fleet must employ if its limiting distribution is to be maintained. If the latter is not known to the vessels, and they operate entirely independently, i.e. there is no exchange of information concerning the size and position of catches, each vessel can proceed only on the basis of the size and position of its own catches. Since the limiting distribution of effort is that which results in a uniform density of fish over the whole of the fished area, there will be a continual tendency for the distribution of vessels to become uniform, and hence to depart from the required distribution. As soon as any appreciable departure from the limiting distribution has occurred, however, the density of fish will no longer be uniform, and the information on this obtained by the vessels from their independent searching would counteract the tendency towards a uniform distribution of effort in the fished area. Thus a balance will be set up with the fleet generating a somewhat smaller fishing mortality than that corresponding to the limiting distribution, the difference depending primarily on factors such as the relative rate of movement of fish and vessels. On the other hand, if catch information is exchanged by all vessels a closer approach to the limiting distribution could be achieved, since each would have a synoptic picture of the density in the fished area and would not have to search in a more-or-less haphazard manner. A fleet of a given size within which there is communication enabling it to fish with co-ordinated tactics can therefore exert a greater fishing mortality, and hence under certain conditions obtain a greater total catch, than if the vessels searched independently. How much greater will depend on factors such as the speed of the communication and response, and on the exact nature of the response.

Now even with a perfect system of communication it does not follow that in practice the greatest fishing mortality would be generated by a fleet attempting to attain the limiting distribution. To take a simple example, we can suppose that the dispersion rate of fish is the same in all parts of the area, so that in the absence of fishing the density would be uniform. The limiting distribution of effort would in this case also be uniform, but for the same number of vessels to be actively fishing in all parts of the area at any given moment would require that the number of vessels making voyages to the more distant grounds is greater than to the nearer grounds, to compensate for the greater proportion of each voyage that is spent steaming to and from the former compared with the latter. Suppose, then, that the distribution of vessels is changed slightly so that each fishes a little nearer to port than before, the new distribution being that which produces the greatest mortality that is possible within this restriction. The distribution of effort would no longer be uniform, nor limiting, but because the average distance from port at which the vessels are working is now smaller, the same number of vessels would be able to spend more time actually fishing. Thus the total fishing effort exerted by the fleet would increase, and this may well more than compensate for its distribution being no longer limiting, and result in an even greater mortality being generated. The situation is shown diagrammatically in Figs. 10.4. Fig. 10.4.1 shows an hypothetical example of the fishing mortality generated per unit fishing effort as a function of the average distance from port at which vessels are working, the distribution at each distance being that which produces the greatest mortality; the dotted line A is the maximum of the curve and corresponds to the limiting distribution of effort. Fig. 10.4.2 gives an example of the type of relationship that might be expected between the total effort that a given number of vessels can exert and their average distance from port. The fishing mortality actually generated by a given sized fleet, as a function of the average distance from port, is the product of these two curves, and is shown in Fig. 10.4.3. The maximum mortality is generated when the average distance from port is less than that corresponding to the limiting distribution of effort. It will be noted that the shape of the curve of Fig. 10.4.1 depends on the rate of dispersion of fish and, in the more complex situations which arise in practice, on variations in this rate from one place to another within the whole area, i.e. on the distribution of centres of aggregation. The curve of Fig. 10.4.2, on the other hand, depends also on the location of the centres of aggregation relative to the port or ports on which the vessels are based.

Now, if the *fleet* is distributed so as to generate the highest possible fishing mortality, the effect will be that the density of fish (and hence the catch per unit fishing time) is not uniform in all the fished area, as it would be if the distribution of *effort* is limiting; the density will in fact be lower on the grounds nearer to port than on the more distant one. The distribution of vessels that is required to generate the greatest mortality, and hence to obtain the greatest catch, is very close to that which results in the *catch per trip* being the same for all vessels; the higher density on the more distant grounds compensating for the greater proportion of each trip which is spent in steaming to and from them. As in the case of the concept of optimum fishing discussed in §19.1, the problem is ultimately an economic

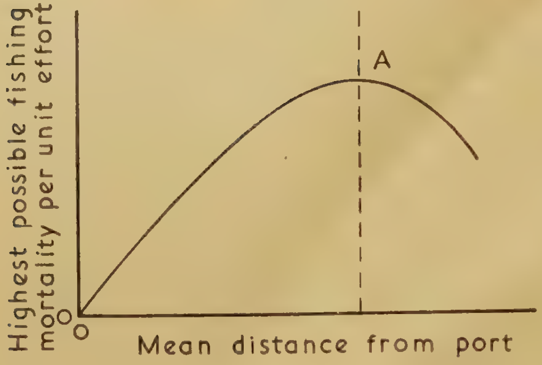

Fig. 10.4.1 Relationship between the highest possible fishing mortality generated per unit fishing effort and mean distance of vessels from port. The point A corresponds to the limiting distribution of effort.

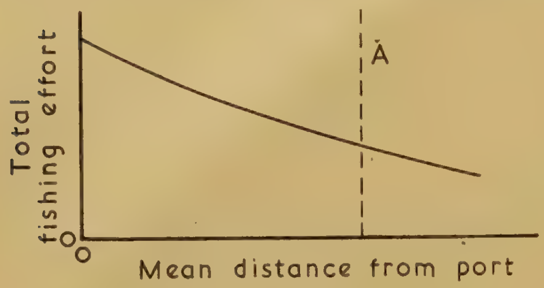

Fig. 10.4.2 Relationship between fishing effort generated by a fleet of a given size and mean distance of vessels from port.

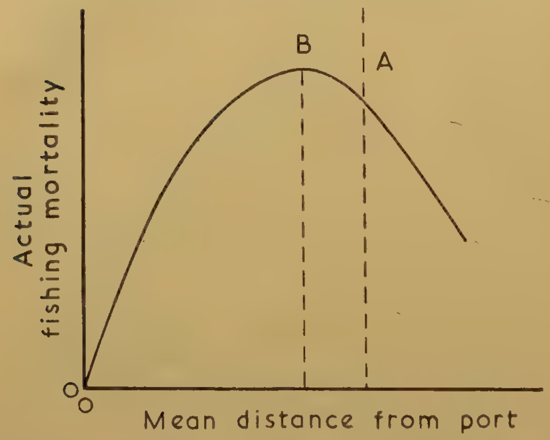

Fig. 10.4.3 Relationship between highest possible fishing mortality generated by a fleet of a given size and mean distance of vessels from port. The maximum mortality (point B), corresponding to the optimum fishing tactics, occurs at a mean distance rather lower than that for the limiting distribution of effort (point A).

FIGS. 10.4 LIMITING DISTRIBUTION OF EFFORT AND OPTIMUM FISHING TACTICS

[Hypothetical examples of possible relationships between the fishing mortality generated by a given effort, with the fleet operating at various distances from port. In each case the distribution of vessels is assumed to be as effective as possible for the stated mean distance of vessels from port.]

one; if decreasing the average distance even further reduced the cost of fishing more than the resulting loss in value of the catch, economic incentive would cause vessels to make the necessary change in their distribution.

Further practical considerations arise when it is remembered that hitherto we have been regarding the aggregating tendencies of the fish to be unchanging. Now in reality they rarely form aggregations which remain stationary in form or position for long periods, and even in a relatively static population such as the North Sea plaice there are continual shifts in the centres of density as well as an extensive winter spawning migration. In these circumstances the distribution of the fleet required to generate the greatest mortality will itself be changing with time and will be, to a greater or lesser extent, unpredictable. The question of the best searching tactics for vessels to adopt in order to attain the best distribution therefore becomes important, as do the effects of exchange of information and co-ordinated fishing tactics. For example, where changes in distribution of fish are not rapid and there is a steady flow of vessels to and from the fishing grounds, exchange of information may mean that each vessel as it leaves port can proceed to the best grounds without spending too much time searching. Nevertheless, it will nearly always be necessary to allow for some time spent in searching, and this must be taken into account when establishing the total effort that can be generated by a fleet of a given size. Clearly, it would be undesirable for so much time to be spent in steaming—either in searching or in responding to information—that the total effort of the fleet becomes unduly reduced.

Thus we are led to the concept of the *optimum fishing tactics* defined as those which, in practice, enable the greatest fishing mortality to be generated by a fleet of a given size. Essentially, the optimum would be a compromise between the requirements for the limiting distribution of effort on the one hand, and, on the other, practical considerations such as the need to avoid an excessive proportion of vessels' sea-time being spent in steaming, or in searching for fish in areas where the occurrence of high concentrations is possible but unlikely. Thus optimum tactics might imply division of labour—temporary or permanent—between those vessels fishing and those searching, which would probably be most effective where there are rapid changes in the distribution of fish and echo-survey could be used.

The determination of the best tactical system in a given case is clearly not a simple problem, though a rough estimate might not be difficult to deduce. The main data required are the rates of dispersion of fish and their variations in time and space, which could be obtained by methods such as those of §14.1.2.4. For future work on this problem, one essential is an index by means of which observed or other possible tactics can be compared quantitatively, and we suggest that this could be in terms of the fishing mortality generated when they are employed. Now, the smallest mortality that a fleet of a given size and working normally could generate (i.e. excluding the deliberate avoidance of high concentrations of fish), is when its activity is distributed uniformly without regard to the distribution of the fish. If we designate the coefficient of this mortality by $\bar{F}$ and that corresponding to the best tactics by $\tilde{F}_{\text{opt.}}$, then a suitable index of the efficiency of the actual tactics which have produced the observed effective overall coefficient $\tilde{F}$ is the ratio

$$\frac{\tilde{F} - \bar{F}}{\tilde{F}_{\text{opt.}} - \bar{F}} \quad \cdots \quad \cdots \quad \cdots \quad \cdots \quad (10.43)$$

The difference between $\tilde{F}_{\text{opt.}}$ and $\bar{F}$ is largely dependent on the degree of aggregation of the fish. It will be least if the rate of dispersion of fish is the same in all parts of the area, in which case the optimum tactics would be a nearly uniform distribution of vessels, actually with some decrease of fishing intensity with increasing distance from port. It will be noted that the index (10.43) can be greater than zero without there being co-operation of any kind between individual vessels. Thus if each vessel operates independently and searches by tending to stay longest in those areas where it happens to find the greatest concentration of fish, a mortality coefficient will be generated by the fleet which we may call $\tilde{F}_{\text{ind.}}$. An index of co-operation can therefore be defined to measure the additional mortality as the result of exchange of information and response to it, as

$$\frac{\tilde{F} - \tilde{F}_{\text{ind.}}}{\tilde{F}_{\text{opt.}} - \tilde{F}_{\text{ind.}}} \quad \cdots \quad \cdots \quad \cdots \quad \cdots \quad (10.44)$$

The situation corresponding to $\tilde{F}_{\text{ind.}}$ will be seen to be very similar to that which we have discussed in §10.2.4 in connection with the food searching behaviour of a fish population, since in this case we assumed that there was no form of communication between individual fish concerning the whereabouts of food aggregations.

In §19.1 we discuss the concept of *optimum fishing* as the ultimate objective of fishery regulation. No generalised statement of all the requirements for optimum fishing can be made, but we suggest that implicit in the concept—in whatever circumstances it may be applied—is the premise that the fishing fleet operates with as high an economic efficiency as is compatible with other considerations. One contributing factor will always be the system of fishing that is adopted, though its importance will depend greatly on the type of fishery in question. In the North Sea, at least, the operation of exploiting the fish populations is not conceived as a whole and is largely competitive, though there is some degree of co-operation between vessels. It may well be that the present system of fishing is very nearly the best method, or that some division of function between searching and actual fishing would be advantageous, though if the latter practice were adopted vessels could no longer be economically independent—the fishing unit would be a group of vessels or even an entire fleet instead of a single ship. Whatever may be the answer to these questions the subject would seem to merit further investigation, and we suggest that this might profitably be on the basis of an objective assessment of the values of various possible tactics in terms of the resulting mortality coefficients, and possibly by means of some such indices of efficiency as suggested above.

SECTION 11: MIXED POPULATIONS—THE ANALYSIS OF COMMUNITY DYNAMICS

In this paper we have hitherto dealt with populations consisting of a single species, but many exploited areas contain more than one species of commercial importance, and often these are caught simultaneously by the particular gear in use. In such cases we are interested in the effect of different characteristics of fishing intensity on the combined yield of all species, weighted if necessary by their relative values, and in this section we discuss briefly the procedures applicable to fisheries based on mixed populations. Strictly speaking, the behaviour of all fish populations inhabiting the same water basin is to some extent interrelated, since all are ultimately dependent on the productivity of the primary producer organisms of that area. It is only when there is direct interaction between two or more populations (§11.2) that special methods of analysis are essential, and in many instances there may be populations in the same area which, at least from the point of view of their exploitation, may be treated as effectively independent of each other (§11.1).

11.1 Independent Populations

As far as effectively independent populations are concerned two cases may be distinguished, according to whether each population supports a completely independent fishery or whether similarities in the ecological niches and in the behaviour of the fish result in them being caught simultaneously by the same fishing gear. In the former case, there will be a set of exploitation equations for each population, and none of these sets will contain any parameters referring to the existence of the remaining populations. The methods already described can therefore be applied separately to each population, and need no modification. If, on the other hand, there are two or more populations which, though themselves effectively independent, are nevertheless caught by the same fishing operations, a given total effort will exert a fishing mortality F_A (say) on population A, and, in general, a different fishing mortality on each of the remaining populations, say F_B on population B, F_C on population C, and so on. If any changes in the total fishing effort do not involve changes in its spatial distribution, the fishing mortality on each population will change in the same ratio, and we can write

$$F_A = r_B F_B = r_C F_C = \dots \text{etc.}$$

where r_B, r_C, . . . etc. are constant for all values of the fishing effort, and depend on the relative efficiency of the gear in question for each species with respect to population A.

Where each of the various populations inhabiting the exploited area tends to aggregate in different parts of that area, it is known that vessels may take advantage of a knowledge of these differences to obtain certain species in preference to others. In such a case, a change in total fishing effort would be expected to result in a change in the relative abundance of the different species, and hence in the *distribution* of fishing effort. For example, an increase in total effort might result at first in a relatively greater mortality in the more preferred species; these would then become relatively scarcer, and a higher proportion of the total effort would be diverted to those areas where the less preferred species were more abundant.

By the methods of §10.2.3 we may calculate from data for the catch of each species and the fishing intensity in each sub-area, values of $\bar{\tilde{f}}_A$, $\bar{\tilde{f}}_B$, $\bar{\tilde{f}}_C$ etc., the effective overall intensities relating to each species. In any one year we should expect to find differences between these values, the highest being for those populations whose concentrations corresponded most closely with the areas of high fishing intensity. The extent to which these differences are related to a deliberate searching for preferred species might be measured by comparing series of estimates of $\bar{\tilde{f}}_A$, $\bar{\tilde{f}}_B$, etc. obtained under different conditions of fish abundances or fishing effort. Denoting the latter by the prefixes $_1$, $_2$ etc., then the condition

$${}_1\bar{\tilde{f}}_A : {}_2\bar{\tilde{f}}_A : \text{etc. as } {}_1\bar{\tilde{f}}_B : {}_2\bar{\tilde{f}}_B : \text{etc.}$$

expresses the null hypothesis that all species are equally sought. Analysis of departures from such proportionality could indicate the extent to which knowledge of the location of areas in which some species were partially segregated was being used effectively to concentrate fishing on the more highly prized fish.

11.2 INTERDEPENDENT POPULATIONS

The interaction between two or more species has been dealt with by a number of workers in this field, to whom some reference has been made in previous sections. Apart from the fact that no treatment has been given, as far as we know, of the case in which one or more of the interacting populations are exploited, the classical methods of analysis such as are summarised by Kostitzin (1939) involve simplifying assumptions and procedures which are unacceptable for the present purpose. For example, no reference is made to the size composition of the populations or the growth of the individuals concerned, and when this is done procedures such as taking the mortality caused by predation to be proportional to the product of the number of individuals in the predator and prey populations are clearly inadequate. The treatment given here can be regarded only as a tentative introduction to the subject, but certain important problems that arise when attempting to set up theoretical models of interacting populations have already been discussed in §9.4.3.2.3, notably the method of representing the grazing power of a predatory population, and for the most part it will be sufficient to take the treatment only to the stage at which the methods of that section become directly applicable.

The principal mechanisms of interaction between fish populations that are likely to be met with are competition for food and direct predation; in the following analysis we deal briefly with simple examples involving one or other of these. From the theoretical point of view these mechanisms need not involve populations of taxonomically distinct species. For example, one section of a population may be predatory on another section of the same population ('cannibalism') and this will render heterogeneous the population as a whole. Again, considerable differences between the sexes in growth rate and the age at which maturity occurs have been demonstrated in many species of fish and sexual heterogeneity may extend, in some cases, to natural and fishing mortality rates. If these differences are small, it is usually sufficient to take mean values for parameters, and to treat the population as a single unit. If they are large, on the other hand, and because the feeding habits of both sexes are likely to be very similar, the exploitation of such a population presents problems essentially similar to the simultaneous exploitation of two taxonomically distinct populations competing for the same food supply. A further situation which may often occur is that of one or more phases of a population feeding on different food from the rest. For example, feeding habits may become progressively less specialized with age, so that food may be in limiting supply for young fish but not for old, and hence the growth of only the former appreciably affected by density; this is sufficient to render the population heterogeneous with respect to growth, but no special methods are required for the analysis of this situation beyond those already given in §9.2, when discussing variations in growth with age.

The examples discussed in this section are therefore of competition for a common food supply between two populations having different dynamic characteristics (§11.2.1), and of an inter-specific system of one population predatory on another (§11.2.2). In both these cases we shall assume that interaction is confined to the post-recruit phase.

11.2.1 *Competition for a common food supply*

We consider a system in which two fish populations or population units, designated as 1 and 2 with parameters having these suffixes, are both feeding exclusively on the same food. If we have data for two states in each of which the populations are steady but at different levels of density corresponding, for example, to two levels of fishing intensity, then with the methods and terminology of §9.4.3.2.3 we can express the total annual food consumption of both populations for the first of those states as

$${}_1\Xi_{1+2} = r\omega\left(1 - e^{-(G_1 + G_2)\lambda'}\right) \quad \ldots \quad \ldots \quad \ldots \tag{11.1}$$

that consumed by population 1 being

$${}_1\Xi_1 = \frac{G_1\, r\omega}{G_1 + G_2}\left(1 - e^{-(G_1 + G_2)\lambda'}\right) \ldots \quad \ldots \quad \ldots \tag{11.2}$$

and that by population 2 being

$${}_1\Xi_2 = \frac{G_2\, r\omega}{G_1 + G_2}\left(1 - e^{-(G_1 + G_2)\lambda'}\right) \ldots \quad \ldots \quad \ldots \tag{11.3}$$

Similarly, for the second steady state we have

$${}_2\Xi_{1+2} = r\omega\left(1 - e^{-({}_2u_1 G_1 + {}_2u_2 G_2)\lambda'}\right) \quad \ldots \quad \ldots \tag{11.4}$$

$${}_2\Xi_1 = \frac{{}_2u_1\, G_1\, r\omega}{{}_2u_1\, G_1 + {}_2u_2\, G_2}\left(1 - e^{-({}_2u_1 G_1 + {}_2u_2 G_2)\lambda'}\right) \quad \ldots \tag{11.5}$$

and

$${}_2\Xi_2 = \frac{{}_2u_2\, G_2\, r\omega}{{}_2u_1\, G_1 + {}_2u_2\, G_2}\left(1 - e^{-({}_2u_1 G_1 + {}_2u_2 G_2)\lambda'}\right) \quad \ldots \tag{11.6}$$

In these latter equations, the change in the grazing power of each population, relative to the values applying in the first steady state, G_1 and G_2, is given respectively by the factors

$${}_2u_1 = \frac{{}_2\Xi_1\left(1 - \dfrac{{}_2\Xi_1}{{}_2\Xi_{L1}}\right)}{{}_1\Xi_1\left(1 - \dfrac{{}_1\Xi_1}{{}_1\Xi_{L1}}\right)} \quad \ldots \quad \ldots \quad \ldots \tag{11.7}$$

and

$${}_2u_2 = \frac{{}_2\Xi_2\left(1 - \dfrac{{}_2\Xi_2}{{}_2\Xi_{L2}}\right)}{{}_1\Xi_2\left(1 - \dfrac{{}_1\Xi_2}{{}_1\Xi_{L2}}\right)} \quad \ldots \quad \ldots \quad \ldots \tag{11.8}$$

With a knowledge of the parameters of each population in each state, estimates of all the quantities in (11.7) and (11.8) can be obtained in the usual way from (9.32) and (9.34), using parameters appropriate to each population and state.

Now, from (11.2) and (11.3) we have

$$G_2 = \frac{{}_1\Xi_2}{{}_1\Xi_1}\, G_1$$

and substituting in (11.1) gives

$$ {}_1\Xi_{1+2} = r\omega(1 - e^{-G_1\lambda'(1 + {}_1\Xi_2/{}_1\Xi_1)}) \quad .. \quad .. \quad .. \quad (11.9) $$

Performing similar operations on (11.4), (11.5) and (11.6) gives

$$ {}_2\Xi_{1+2} = r\omega(1 - e^{-{}_2u_1 G_1\lambda'(1 + {}_2\Xi_2/{}_2\Xi_1)}) \quad .. \quad .. \quad (11.10) $$

and (11.9) and (11.10) provide solutions for the unknown quantities $r\omega$ and $G_1\lambda'$. For any other steady state, say that corresponding to a different level of fishing mortality in one or both populations, we have a further set of equations homologous with those above and which contain only two unknown quantities, i.e. ${}_xW_{\infty 1}$ and ${}_xW_{\infty 2}$ specifying the growth rate in each population, for which simultaneous solutions can therefore be obtained. With these growth parameters thus determined, the yield from each population in the new steady state can be assessed by means of (4.4) in the usual way. These methods may be extended to deal with systems involving more than two populations competing for the same food supply, or by the methods of §9.4.3.2.4, to two or more population units feeding on two or more species of food organisms.

The above methods have a bearing on the practical problem of obtaining an index of the competition between two species for the same food organisms. Shorygin (1946) has proposed a formula which, in the simple case of two predator populations feeding exclusively on a single population of food organisms, is

$$ \Gamma \doteq \frac{a_1 + a_2}{b} $$

where Γ denotes the index of competition, or the 'force of concurrence' as he terms it, a_1 and a_2 are the daily consumption of the food by the two populations, and b is an instantaneous measure of the standing crop of the food population. It can be seen that Γ is, in effect, a rough measure of the total instantaneous grazing mortality coefficient $(G_1 + G_2)$ caused by both predators. Shorygrin was led to use an instantaneous measure of competition because he did not have sufficient information to evaluate the production of the food organisms over a long period, but it is doubtful whether this is a valid method. Thus it is difficult to imagine competition occurring instantaneously, for the same reason that individual vessels of a fleet do not compete with each other at one and the same instant (§8.3.1). On the contrary, competitive influence is manifest in terms of the consumption of food organisms that has occurred as the result of previous grazing activity, and depends also on the 'non-grazing' mortality in the food organisms (which we denote in terms of the life-span λ'). Moreover, it is desirable to distinguish between the competitive effect of population 1 on population 2, and vice-versa.

We would suggest that a better approach to this problem might be to define the ratio of the amount of food actually consumed by one population (in the face of competition from the other) to that which it would have consumed in the absence of the other population. Taking first population 1, we can denote these quantities by Ξ_1 and $\Xi^0{}_1$, where Ξ_1 is given by (11.2), but $\Xi^0{}_1$ is given by

$$ \Xi^0{}_1 = r\omega\,(1 - e^{-G_1\lambda'}) $$

Denoting the competitive effect of population 2 on population 1 by ${}_1\Gamma_2$, we can put

$$ {}_1\Gamma_2 = 1 - \frac{\Xi_1}{\Xi^0{}_1} = 1 - \frac{G_1}{G_1 + G_2} \cdot \frac{(1 - e^{-(G_1+G_2)\lambda'})}{(1 - e^{-G_1\lambda'})} \quad .. \quad (11.11) $$

Similarly, for the competitive effect of population 1 on population 2 we have

$$ {}_2\Gamma_1 = 1 - \frac{\Xi_2}{\Xi^0{}_2} = 1 - \frac{G_2}{G_1 + G_2} \cdot \frac{(1 - e^{-(G_1+G_2)\lambda'})}{(1 - e^{-G_2\lambda'})} \quad .. \quad (11.12) $$

We may note first that the index of competition defined in this way varies between 0 and 1, since

$$ {}_1\Gamma_2 \to 0 \text{ as } \Xi_1 \to \Xi^0{}_1 $$

and

$$ {}_1\Gamma_2 \to 1 \text{ as } \Xi_1 \to 0 $$

This is a convenient property, but we must now examine the behaviour of ${}_1\Gamma_2$ and ${}_2\Gamma_1$, in terms of the abundance of the two competing populations.

(i) If the abundance of population 2 is much less than that of 1, so that $G_2 \ll G_1$, we find from (11.11) that

$$ {}_1\Gamma_2 \to 0 $$

i.e. that the competitive effect of 2 on 1 tends to zero. In similar circumstances, from (11.12),

$$ {}_2\Gamma_1 \to 1 - \frac{1 - e^{-G_1\lambda'}}{G_1} $$

and if the *absolute* value of G_1 is large, as well as being large relative to G_2, then

$$ \frac{1 - e^{-G_1\lambda'}}{G_1} \to 0 $$

so that

$$ {}_2\Gamma_1 \to 1 $$

the implication being that the competitive effect of 1 on 2 in these circumstances is very great, which is the required conclusion. The reverse behaviour is obtained if $G_2 \gg G_1$

(ii) If both populations are small, so that the absolute values of G_1 and G_2 are small, we have

$$ 1 - e^{-(G_1 + G_2)\lambda'} \simeq (G_1 + G_2)\lambda' $$

Hence, from (11.11),

$$ {}_1\Gamma_2 \to 0 $$

and also, from (11.12)

$$ {}_2\Gamma_1 \to 0 $$

Thus, if both populations are small their mutual competitive effect is also small.

(iii) Finally, if both populations are large, so that the absolute values of G_1 and G_2 are large, then

$$ 1 - e^{-G_1\lambda'} \to 1 $$

and

$$ 1 - e^{-G_2\lambda'} \to 1 $$

Hence

$$ {}_1\Gamma_2 \to 1 - \frac{G_1}{G_1 + G_2} = \frac{G_2}{G_1 + G_2} $$

and

$$ {}_2\Gamma_1 \to 1 - \frac{G_2}{G_1 + G_2} = \frac{G_1}{G_1 + G_2} $$

Thus we find that both the relative size of G_1 and G_2 and also their absolute values must be taken into account to define the measure of the competitive effect of one population on the other which we have suggested above. Furthermore, the non-grazing mortality in the food population, which in the above treatment is represented approximately by the value of λ,′ also plays a part in determining the competitive effect. Admittedly, the index we suggest is more difficult to determine in practice than that used by Shorygin, though this author was able to obtain estimates of the food consumption and standing crop in absolute units which at once give estimates of G_1 and G_2. The above analysis indicates that a true measure of competition requires considerable knowledge of the dynamics of the system and its components, and that approximations for practical use should be examined in the light of an analytical treatment of this kind.

11.2.2 *One population predatory on another*

We now discuss an interspecific predator-prey system consisting of population 1 feeding on population 2, both being exploited. Basically, this is, of course, the same system as that of a fish population grazing on an invertebrate food, which we examined in §9.4.3.2.3. The main differences derive from the need in the present context to formulate the dynamic characteristics of the prey population in detail, partly because the simplifying assumptions adopted previously are unlikely to be tenable if the prey is fish, and also because we are supposing that the latter are commercially important and that the yield from them is to be evaluated.

We denote by G_1 the mortality rate in population 2 caused by the predatory activity of population 1, this mortality forming, of course, part of the 'natural' mortality of population 2. For a given observed state in which the populations are in equilibrium with each other and with the fishing activity, the yield from population 1 is given in the usual way, i.e.

$$(Y_W)_1 = F_1 R_1 e^{-M_1\rho_1}(W_\infty)_1 \sum_{n=0}^{3} \frac{\Omega_n e^{-nK_1(t_{\rho'1}-t_{0\,1})}}{F_1+M_1+nK_1}\left(1-e^{-(F_1+M_1+nK_1)\lambda_1}\right) \quad .. \quad (11.13)$$

That from population 2, however, is

$$(Y_W)_2 = F_2 R_2 e^{-(G_1+M_2)\rho_2}(W_\infty)_2 \sum_{n=0}^{3} \frac{\Omega_n e^{-nK_2(t_{\rho'\,2}-t_{0\,2})}}{F_2+M_2+G_1+nK_2}\left(1-e^{-(F_2+M_2+G_1+nK_2)\lambda_2}\right) \quad (11.14)$$

The weight of population 2 consumed annually by population 1, or, in other words, the 'yield' from population 2 obtained by population 1, can be written as

$$\Xi_1 = G_1 R_2 (W_\infty)_2 \sum_{n=0}^{3} \Omega_n e^{-nK_2(t_{\rho 2}-t_{0\,2})} \left\{ \frac{1-e^{-(M_2+G_1+nK_2)\rho_2}}{M_2+G_1+nK_2} + \frac{e^{-(M_2+G_1+nK_2)\rho_2}}{F_2+M_2+G_1+nK_2}\left(1-e^{-(F_2+M_2+G_1+nK_2)\lambda_2}\right)\right\} \quad .. \quad (11.15)$$

which is analogous to (9.38).

From data for one steady level of population 2 we could not distinguish between M_2 and G_1 of (11.14), since any estimate of the 'natural' mortality rate of this population would give the combined values of M_2 and G_1. However, since we are postulating that Ξ_1 of (11.15) forms the whole of the food consumption of population 1, it can be calculated in the usual way from (9.32), and then (11.15) will provide a solution for G_1. If, now, a different fishing mortality or mesh size is applied to one or both populations, the predatory rate G_1 will change to ${}_xuG_1$ where

$${}_xu = \frac{{}_x\Xi_1\left(1-\dfrac{{}_x\Xi_1}{{}_x\Xi_{L\,1}}\right)}{\Xi_1\left(1-\dfrac{\Xi_1}{\Xi_{L\,1}}\right)}$$

(cf. (9.44))

However, ${}_x\Xi_1$ will be given by the appropriate form of (11.15) and (9.32), and ${}_x\Xi_{L\,1}$ by (9.34). Then the only unknown quantity appearing in these equations is ${}_xW_{\infty\,1}$ specifying the new growth rate in population 1, which is therefore computable.

In the above equations (and, in fact, in all those of this section) recruitment is taken for simplicity to be constant, so that interaction between predator and prey is restricted to the mortality and growth of individuals in the post-recruit phase. If, however, recruitment into each population is expressed in terms of egg-production, the system formulated by (11.13) and (11.14) becomes self-regenerating. For purposes of illustration we may suppose that larval mortality in the predatory population conforms to the intraspecific density dependent mechanisms formulated by (6.10), so that predator recruitment can be written as

$$R_1 = \frac{1}{\alpha + \beta/E_1} \quad \dots \quad \dots \quad \dots \quad \dots \quad (11.16)$$

Further, predator egg-production can be taken as proportional to the total weight of mature females, and with the terminology of §6.1.2 is

$$E_1 = s_1\chi_1\,({}_\eta\bar{P}_W)_1 \quad \dots \quad \dots \quad \dots \quad \dots \quad (11.17)$$

Now ${}_\eta\bar{P}_W$ (given in full by (6.18) or (6.19)) depends, in particular, on the rate of growth of the predators, which is defined by the value of the same growth parameter $(W_\infty)_1$ as that appearing in (11.13) for $(Y_W)_1$. But $(W_\infty)_1$ is itself a function of the consumption of prey by the predators, Ξ_1, since it appears in (9.32) used to compute this quantity in the way described above. Hence the self-regenerating form of the predator-prey model defined by the above set of equations incorporates the two primary effects of interaction in such systems, namely (a) the effect of grazing by the predator on the abundance of prey, and (b) the effect of the amount of prey consumed on the reproductive rate of the predator. In this sense it is comparable with the classical predator-prey systems set up by Lotka (1925) and Volterra (1928), in which, however, interaction is represented by a grazing mortality that is proportional to the product of the total numbers of predator and prey, and a reproductive rate in the predator population that is directly proportional to the number of prey. As understanding of the dynamics of populations has advanced in recent years, several authors have pointed out that these assumptions involve extreme simplification and are unacceptable as generalisations of the mechanisms of interaction between real populations (Ivlev, 1945, F. E. Smith, 1952). Lotka's and Volterra's theoretical models are perhaps best regarded not as generalisations but as very special cases; moreover, the concept of a generalised theory of population dynamics is probably premature and may even be illusory. If studies of animal communities are to have an adequate theoretical background —and we suggest that this is essential for a proper understanding of the complex phenomena involved—it would seem better in the first instance to develop models according to the properties of particular systems, rather than to attempt to set up a general theory. That is not to say that every system must be regarded as entirely unique. Generalisations have to be made at some stage and continued search for them remains of the greatest importance for the disciplined progress of work on animal populations; but they should emerge as syntheses of knowledge of a range of actual cases if the danger of producing theoretical models having no counterpart in nature is to be avoided.

The theoretical systems outlined here are still, of course, much simplified representations of competition and predation of a particular type, but it may be that the simplifications concern mainly the number of interacting populations rather than the mechanisms of interaction. We offer them as a contribution to the formulation of the principal interactions in marine communities.

PART III

Estimation of Parameters

The remainder of this paper is devoted to an application of the theoretical methods developed in Parts I and II. The subject is conveniently considered in two stages, the first dealing with estimation of parameters (Part III), and the second with the use of population models containing these parameters to investigate the reactions of fish populations to exploitation (Part IV).

The species with which we shall be primarily concerned is the plaice (*Pleuronectes platessa* L.) of the North Sea. This population has reasonably well defined geographical limits and does not undertake extensive migrations beyond them. It supports an important fishery which is continued throughout the year, the main countries concerned being England, Denmark and Holland; the gear used is primarily the otter-trawl.* Research on North Sea plaice has been going on since the beginning of the century, in the early years of which the main features of the biology of the species were established. It was not until 1929, however, that regular market sampling for age-composition and growth rate began in this country, so that a detailed investigation along the lines we shall attempt must start from this time. The period between 1929 and 1938 was one during which the plaice population was in a fairly steady state, and the values of the majority of the parameters which we shall determine refer to this period. We also make use of data, both published and unpublished, referring to the effects of the 1939-45 war on the plaice stocks and, in addition, certain recent information collected since 1945, including some of the results of the plaice marking experiments started in 1946.

Although information relating to the North Sea plaice population and its associated fishery is extensive and, in general, of a type suitable for the present investigation, we have found that it is not sufficient to illustrate adequately certain of the methods which we believe to be important in the analysis of demersal fisheries, and there are certain relevant phenomena which cannot be studied using the plaice data at present available. In order, therefore, to make the practical aspect of this investigation more balanced we have drawn on information relating to another important demersal species of the North Sea, namely the haddock (*Gadus aeglefinus* L.). The haddock occurs mainly in the northern part of the North Sea and its distribution does not overlap that of the plaice to any great extent, but the two fisheries have some important features in common. Thus the North Sea haddock population, like the plaice, has reasonably well defined limits and seems to behave as one unit; it also supports a major fishery in which the gear most frequently used is the otter-trawl. Extensive quantitative data for the haddock date from 1923, and from then until the present time (with the exception of the 1939-45 war period) population surveys by a research vessel have formed a regular part of the research on this fish. Haddock research is carried out from Aberdeen by the staff of the Marine Laboratory of the Scottish Home Department, so that the present authors do not have first-hand knowledge of the data. Consequently, the material used will be restricted almost entirely to published information, and then only to that referring to the pre-war period during which the haddock fishery was effectively stabilised. We would stress that our use of haddock data is essentially for the purpose of illustrating methods for the determination of parameters and the effect of certain phenomena on the behaviour of population models, though it will be appreciated that this entails making approximate estimates of most parameters which appear in the models, in addition to those relating to the particular relationship which it is desired to illustrate.* In those sections of Part III where the main parameters are determined we have therefore found it convenient to treat the plaice and haddock data in parallel.

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*In recent years there has been a marked increase in the use of the Danish seine in the North Sea plaice fishery, but this gear was of only minor importance during the period between the two world-wars with which we are primarily concerned here.

In addition to plaice and haddock data we shall make brief reference in certain sections of Part III to information about other species to help illustrate the application of particular techniques. These references occur especially in §§14.3.2.2, 15.2.3.2 and 16.2.3, dealing respectively with the separate estimation of fishing and natural mortality coefficients, the relationship between egg-production and recruitment, and the estimation of growth parameters.

Some comments relating to the presentation of Part IV will be found in the introduction to that part; here it may be helpful to mention briefly the layout of Part III. The general arrangement is similar to that of Part II in that each major factor is considered in turn, but the order in which these factors are discussed differs to some extent. Thus it is necessary for the application of a number of techniques to have available estimates of the natural and fishing mortality coefficients, so this subject is considered in §§13 and 14, following a preliminary discussion on the standardisation of fishing effort in §12. Included in §14 are several related topics such as the analysis of gear selectivity and of marking experiments, the latter leading to the determination of transport coefficients. §§15 and 16 deal with the remaining factors of recruitment and growth respectively, and in each case mean estimates referring to the pre-war steady states are first determined, followed by attempts where possible to establish the more detailed behaviour of these factors, such as the effects on them of changes in population density.

SECTION 12: RELATIVE FISHING POWER OF VESSELS AND STANDARDISATION OF COMMERCIAL STATISTICS OF FISHING EFFORT

An accurate knowledge of fishing intensity is obviously important in studying the dynamics of a fishery. As will be shown in §§13 and 14, it is a pre-requisite for the estimation of mortality coefficients from age-composition data and from marking experiments in all but the simplest cases, and is an essential part of the methods described in §14.3 for obtaining separate estimates of the fishing and natural mortality coefficients. When using data of fishing intensity for this purpose it is always desirable, and often essential, that they should be expressed in units which bear a constant and direct relation to the resulting fishing mortality coefficients; for example, data containing statistics of actual fishing time would satisfy this criterion only if all vessels had the same fishing power. It is therefore necessary to devote some attention to the problem of adjusting statistics of fishing time to standard units.†

12.1 Definitions and Method

An absolute definition of the fishing power of a vessel can be obtained only in terms of the fishing mortality generated by it. The latter cannot be measured directly, but for purposes of standardising statistics of fishing time it is sufficient to adjust these according to the *relative fishing power* of the vessels in question; this is defined, and can be measured in practice, as the ratio of the catch per unit fishing time of the vessel to that of another vessel taken as a standard and fishing on the same density of fish on the same type of ground. In this way each vessel can be allotted a *power factor*, and in order to obtain a convenient standard unit of fishing time we need to find some permanent characteristic of vessels that is related in a simple way, preferably proportionally, to their power factors, so that large-scale conversion of commercial statistics of fishing time to such units can be achieved without undue labour. This, rather than a detailed analysis of all factors affecting the fishing power of a vessel, is the main purpose of the investigation to be described.

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*A general analysis of the pre-war haddock data is at present being undertaken at Aberdeen, the results of which will show which of the estimates given in this paper may need revision. An application of theoretical models using post-war data has been published by Parrish and Jones (1953) (see §1).

†It will be remembered from §3.3 that we are defining fishing effort as the total fishing time per year, and fishing intensity as the fishing effort per unit area. Each contains statistics of fishing time, and each is therefore standardised if the fishing time of vessels is adjusted according to their fishing powers.

Hickling (1946b) has assessed the 'performance' of trawlers working from Milford Haven fishing for hake, by taking the catch per 100 hours fishing of each vessel averaged over a relatively long period without regard to the positions from which the catches were obtained. A disadvantage of this procedure is that performance is influenced by the contemporary stock abundance, as can be seen from Hickling's Fig. 4 for the years 1938 and 1942 in which the abundance of hake differed greatly. This difficulty could be overcome by selecting one vessel as standard and computing ratios of the catches per 100 hours fishing of all other vessels to it, thus producing indices of 'relative performance' that would be independent of stock abundance. However, relative performance is not necessarily the same as relative fishing power defined above, since it includes any ability that larger vessels may possess to fish better grounds, i.e. where the fish density is higher, than smaller vessels. In one respect this is an advantage, because if a larger vessel does, for this reason, catch more fish than a smaller one, it will exert a correspondingly greater fishing mortality. On the other hand, this ability is not necessarily a permanent characteristic of a vessel, and for the present purposes it seems better to aim at assessing relative fishing power rather than relative performance, and to compute an effective overall fishing intensity as defined in §10.2.3.1 by weighting fishing time adjusted by relative fishing power according to the density of fish in question.

For the present analysis we have therefore made use of the fact that the basic unit of data in the British statistics is a single 'trip', the information available including:—

(a) Name and type of vessel.

(b) Date of landing and duration of trip.

(c) Principal fishing ground and statistical rectangle fished.

(d) Catch in cwts. of each species.

(e) Number of hauls made and their average duration.

This makes it possible to compare the catch per unit fishing time of vessels that were fishing, as far as could be judged, at the same time and place. Admittedly, there is bound to be considerable error in the estimate of any one power factor by this procedure, but at least it is probable that much of the bias can be avoided. For example, it is most unlikely that large ships consistently work a different part of each statistical rectangle from small ships. As will appear below, the random component of variation in power factor values that was introduced by this method, though large, was not so great that it masked the relationships that were being sought between them and various characteristics of the vessels.

Six rectangles were selected for analysis, namely G3, G4, G5, H3, H4 and H5. These are fairly representative of the southern North Sea trawling grounds, and are fished by both Lowestoft and Grimsby vessels; they also cover the greater part of the area in which the post-war plaice marking experiments were carried out. Each was subdivided into nine sub-rectangles, about 100 sq. miles in area, and comparisons were made of the catch of demersal fish per 100 hours fishing in 1946-47 by first-class steam and motor trawlers fishing in the same sub-rectangle at the same time. This procedure involves the assumption that the relative fishing powers of vessels are independent of the grounds fished; for example, if two vessels moved from, say, a sandy to a muddy ground, it is assumed that both would adapt their gear in such a way that the ratio of their fishing powers remained constant. We have also assumed that this ratio is independent of fish density, though the method could be extended to take this into account. Comparing the total catch of demersal fish is a further simplification, though in the present case it has given a result probably not differing greatly from that which would have been obtained using plaice catches alone, since this species comprised the greater part of the catch from the area in question. Eventually, the relative fishing power of vessels could be evaluated, if required, with respect to each of the major species captured in the area; this might well be necessary when standardising the fishing time of fleets tending to concentrate on different species.

The choice of the vessel to be taken as standard is, of course, quite arbitrary, and need not be in any sense an 'average' vessel. The main criterion is, in fact, that it should be the one for which it is possible to make the greatest number of direct comparisons of catch per 100 hours, and in the present case it happened to be a steam trawler 92 feet in length and of 115 tons (gross). In the first instance were calculated the ratios of the catch per 100 hours of this vessel to each of those that had fished in company with it in any of the sub-rectangles considered, about ten in number. The power factors of the latter were thereby obtained, so that each of them could be compared with other vessels which had not fished directly with the original standard vessel. These and subsequent steps can best be illustrated symbolically, in the following way.

Suppose the standard vessel is denoted by A, and that it has fished in company with vessels B and C, though not necessarily at the same time and place in the two cases. The power factors b_1/a_1 and c_2/a_2 are then calculated, a, b and c being the respective catches per 100 hours of the three ships, the numerical suffixes indicating coincidence of time and locality. This process is extended to include vessels fishing at various times in company with B or C, ratios such as

$$\frac{d_3}{b_3}, \frac{e_4}{b_4}, \frac{f_5}{c_5}, \frac{g_6}{c_6}, \quad \ldots.\text{etc.}\ldots.$$

being computed. In addition, as many 'cross-links' as possible of the type b_7/c_7 are noted. Generally, by extending the chain of ratios, a great number—perhaps thousands—of direct and indirect comparisons are possible. For example, an estimate of the power factor of vessel Z might be obtained by the operations

$$\frac{b_1}{a_1} \times \frac{g_{18}}{b_{18}} \times \frac{j_7}{g_7} \times \frac{m_{24}}{i_{24}} \times \frac{z_{12}}{m_{12}}$$

Proceeding in this way a number of estimates of the power factor of each vessel were obtained, care being taken that they were truly independent estimates, that is that no single link was used twice in making two estimates of the same power factor. Thus, given the set of observations $a_1, b_1, a_2, b_2, b_3, c_3$, four possible estimates of the power factor of vessel C are

$$\text{(i)}\ \frac{b_1}{a_1} \times \frac{c_3}{b_3} \quad ; \quad \text{(ii)}\ \frac{b_2}{a_2} \times \frac{c_3}{b_3} \quad ; \quad \text{(iiia)}\ \frac{\frac{b_1}{a_1} + \frac{b_2}{a_2}}{2} \times \frac{c_3}{b_3} \quad ; \quad \text{(iiib)}\ \frac{b_1 + b_2}{a_1 + a_2} \times \frac{c_3}{b_3}$$

These, however, are not independent, and in the absence of a rigorous statistical treatment of the problem the last would probably give as good an estimate as any from these observations. We have used the arithmetic mean of the numerous estimates of the power factor for each vessel in the present analysis, but a desirable refinement would be the allocation of a weighting factor to each estimate of power factor, depending on the error of any given ratio and the number of ratios involved in calculating the estimate. It was found, nevertheless, that the crude method allowed definite conclusions to be drawn concerning the relationship between power factor, gross tonnage and length in the case of steam trawlers, and between power factor, gross tonnage and brake horse power in motor trawlers. We consider first the relationship between power factor and gross tonnage in steam and motor trawlers.

12.2 THE RELATIONSHIP BETWEEN POWER FACTOR AND GROSS TONNAGE IN STEAM AND MOTOR TRAWLERS

When power factors of individual steam trawlers were plotted against tonnage, it was found that there was considerable scatter. This was to be expected in view of the method used, but has no special implications, since much the greater part of the scatter was probably due to methodological error rather than to real differences in the fishing power of ships of a similar tonnage. It did mean, however, that care was necessary in using the data to deduce the relationship between power factor and tonnage. Grouping the data into tonnage classes showed the following two characteristics,

(a) the power factor values tended to increase with tonnage, roughly proportionally;

(b) the standard deviation of the distribution of power factors of each tonnage class also tended to increase roughly proportionally with tonnage.

These two features suggested that a satisfactory way of examining the power factor distribution in more detail, using all the data, would be to compute the power factor/tonnage ratio for each vessel. The distribution of these ratios is shown in the histogram of Fig. 12.1; it is clearly not symmetrical, which is to be expected since the power factors are themselves ratios. It was found, however, that the distribution of logarithms of the power factor/tonnage ratios was fitted adequately by a normal curve; thus calculating the *k* statistics (Kendall, 1948, p. 105) and applying the *t* test gave a value of $t = 0.25$ with a standard error of 0.16. The curve shown in Fig. 12.1 is the log-normal curve having the same geometric mean and log standard deviation as the observed distribution.

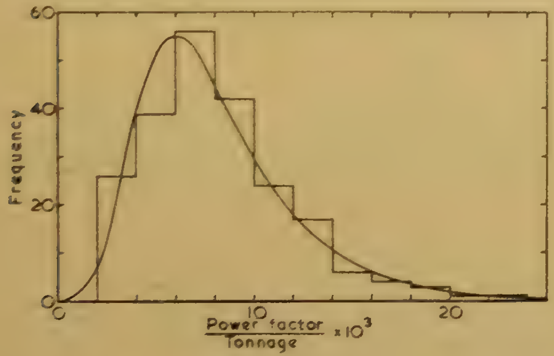


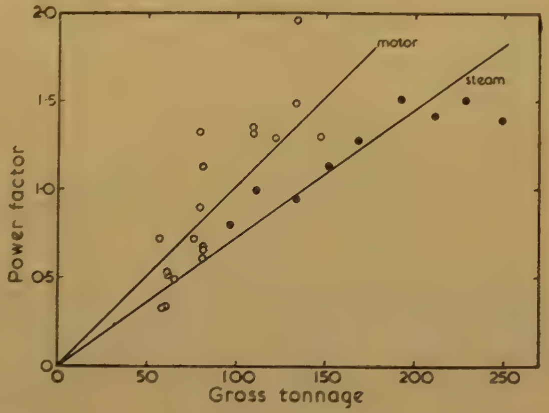
FIG. 12.1 FISHING POWER OF STEAM TRAWLERS

[The histogram shows the frequency distribution of power factor/gross tonnage ratios for steam trawlers. This is not symmetrical but is adequately described by the fitted log-normal curve shown in the figure.]

The fact that the distribution of logarithms of power factor/tonnage ratios did not depart significantly from normality, together with the two features noted above, indicated that a satisfactory representation of the relationship between power factor and gross tonnage in steam trawlers could be obtained by plotting the geometric mean of the power factor values in each 20-ton class against tonnage. The result is shown in Fig. 12.2 (solid circles), the line shown being the best fitting one which passes through the origin. It would appear from inspection that a slightly better fit would be obtained by a line cutting the Y-axis a little above the origin, but it will be remembered that we are trying to find the simplest relationship which gives a reasonably satisfactory fit, and a linear equation would involve much greater difficulties in the conversion of commercial statistics to a standard

FIG. 12.2 FISHING POWER OF STEAM AND MOTOR TRAWLERS

[Power factors of 1st class steam and motor trawlers plotted against gross tonnage. In each case the trend is adequately described by a straight line passing through the origin, indicating that power factor is approximately proportional to gross tonnage.]



form than would a proportional one. A proportional relationship is certainly adequate for the present purposes, the line shown in Fig. 12.2 being calculated from the geometric mean of the individual power factor/tonnage ratios and defined by the equation:

$$P.F. = 0.0073 \times \text{gross tonnage}$$

A similar analysis was carried out for motor trawlers, except that it was necessary to work throughout with individual power factor values since there were too few ships to group into tonnage classes. For comparative purposes these data are shown in Fig. 12.2 (hollow circles), and again a roughly proportional relationship is seen. For motor vessels the equation obtained by taking the geometric mean of the power factor/gross tonnage ratios is:

$$P.F. = 0.0102 \times \text{gross tonnage}$$

It was found that the difference between this constant and the one obtained for steam trawlers is highly significant, so that it can be said that the average fishing power per ton of a motor trawler is some 40% greater than that of a steam trawler.

12.3 THE RELATIONSHIP BETWEEN POWER FACTOR AND LENGTH IN STEAM TRAWLERS, AND BETWEEN POWER FACTOR AND BRAKE HORSE POWER IN MOTOR TRAWLERS

The relationships between power factor and certain other variables were also investigated. Thus in Fig. 12.3 are shown the geometric means of steam trawler power factors for each 5 ft. length class (65′-69′, 70′-74′, etc.). In this case the relationship departs appreciably from proportionality, though it can be represented well by an equation of the form

$$P.F. = a \times (\text{length})^n$$

where *a* and *n* were estimated to be 0.0012 and 1.49 respectively.

The engine power of a vessel might be expected to have a marked effect on fishing power, but unfortunately this is a quantity statistics of which were not readily available for steam trawlers. The brake horse power of motor trawlers was obtainable however, and in Fig. 12.4 the relationship between this and power factor is shown. The line shown in this figure is defined by the equation

$$P.F. = 0.0047 \times B.H.P.$$

obtained from the geometric mean of the (power factor/B.H.P.) ratios.

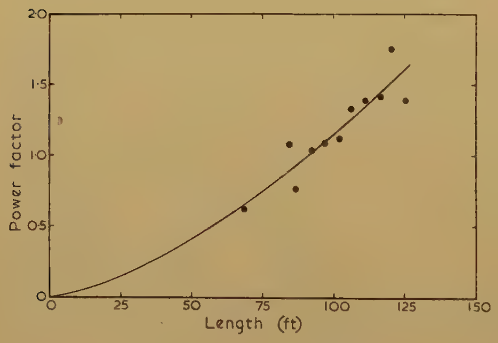


FIG. 12.3 FISHING POWER OF STEAM TRAWLERS

[Plot of power factor against length. This gives a nonlinear trend, so that length is a less convenient index of fishing power than gross tonnage.]

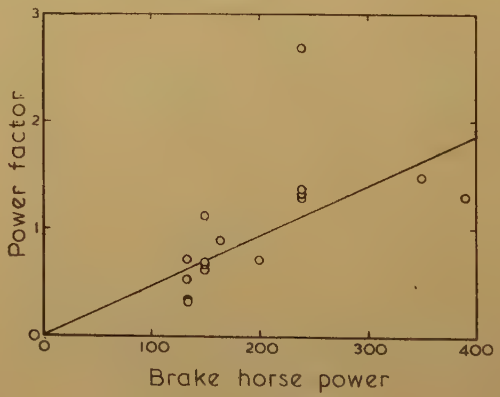


FIG. 12.4 FISHING POWER OF MOTOR TRAWLERS

[Plot of power factor against brake horse power. The data are widely scattered because they refer to individual vessels and not to mean power factors of groups of similar vessels as in steam trawlers; there is, nevertheless, a roughly linear trend.]

12.4 Standardisation of Commercial Statistics

The main conclusion from the above results is that of the factors investigated the gross tonnage of steam trawlers is most nearly proportional to fishing power, and to a degree which would be suitable for purposes of standardising statistics of fishing time. Within the limits of the data a similar conclusion can be drawn in the case of motor trawlers. Hickling, in the paper referred to above, concluded that the performance of steam trawlers was most closely correlated with their tonnage, and in much of his data it would seem that a proportional relationship would be satisfactory. An independent check on the validity of the power factor/tonnage relationships deduced above for steam and motor trawlers is provided by the results of a comparative fishing experiment carried out in the southern North Sea between the research vessels SIR LANCELOT and PLATESSA, the details of which are given by Margetts (1949). The SIR LANCELOT is an oil-fired steam trawler of the Round Table class, of 296 gross tons and 126 feet in length; the PLATESSA is an Admiralty Motor Fishing Vessel of 112 gross tons, 88 feet in length and with a diesel engine of 240 B.H.P. The comparative fishing experiment gave the ratio 1.8 to 1 in favour of the SIR LANCELOT, whereas that predicted from the relationships between power factor and tonnage in steam and motor trawlers given in §12.2 is

$$\frac{296 \times 0.0073}{112 \times 0.0102} = 1.9$$

The two estimates are therefore in close agreement.

In view of these findings we shall take the gross tonnage of a trawler as the most convenient index of its fishing power, and we suggest *thousands of steam trawler ton-hours per year* as a suitable standard unit of fishing effort. Thus the fishing effort of a trawler fleet of Z vessels can be denoted in standard units by the expression

$$10^{-3} \times \sum_{i=1}^{Z} T_i \times h_i \times q_i \qquad \ldots \quad \ldots \quad \ldots \quad (12.1)$$

where T_i is the gross tonnage of vessel i, h_i is the number of hours that it fished during a year, and q_i is a constant relating the fishing power of vessels of the same tonnage but differing in method of propulsion, steam being taken as standard. Thus q is unity for steam trawlers, and equal to $0.0102/0.0073 = 1.4$ for motor trawlers. Similarly, a convenient standard unit of fishing intensity is the *steam trawler ton-hour/sq. nautical mile/year* $\times 10^{-3}$, and this will be used in connection with the analysis of the plaice marking experiments in §14.1.3. The additional labour involved in converting statistics of fishing time of trawlers into standard ton-hour units is therefore that of multiplying the total fishing time of each vessel per year by its gross tonnage, and by a constant in the case of motor vessels, before summing; this would be a rapid and simple routine operation if punched-card and electrical sorting systems are in use. It remains to be seen to what extent the unit would be applicable to other types and nationalities of fishing vessels, or whether some other variable could be found that is even more closely related to fishing power than is gross tonnage. An obviously relevant index is the effective engine power; the brake horse power of motor vessels is a readily available statistic, and it might be possible to obtain data for the shaft horse power of steam vessels, though this would need to be the subject of a further investigation.

Another worthwhile extension of the method described above would be to examine the causes of variation in the power factor values. The three main causes are (a) that due to true variation in fish density, including the effect of errors in the fishing positions as reported in the commercial statistics, (b) varying abilities of skippers and their idiosyncrasies concerning modifications in gear to suit different types of ground, and (c) permanent differences in the fishing power of vessels of the same tonnage and method of propulsion but which are of different classes, design or age. If the last of these components of variation could be distinguished and measured it might enable a more refined technique of standardisation to be developed in which each major class or design of vessel is allotted a factor (i.e. a value of q in (12.1)) to be multiplied by the product of the tonnage of each vessel of the class and its fishing time. This would amount to further sub-division within the broad distinction on the basis of method of propulsion which we have used above, and q would be unity only for steam trawlers of the same group as the standard vessel. A refinement of this kind would in any case be necessary to keep pace with improvements in the efficiency of vessel and gear that may take place in the future, since although there is no reason why, for example, a proportional power factor/tonnage relationship should not be a reasonably permanent feature, the value of the constant of proportionality (i.e. 0.0073 in the case of steam trawlers analysed above) would certainly change if such improvements occurred.*

It can be said, nevertheless, that the standardisation of international fishing time statistics in terms of the steam trawler ton-hour unit by means of (12.1) would greatly enhance the comparative value of such data—a very necessary requirement both for research and regulation in an internationally fished area such as the North Sea.

SECTION 13: ESTIMATION OF THE TOTAL MORTALITY COEFFICIENT $(F + M)$, AND THE MAXIMUM AGE, t_λ

13.1 Methods

Estimates of the total mortality coefficient in fish populations, that is, of the sum of the fishing and natural mortality coefficients, have been obtained by many authors from data of the abundance, either relative or absolute, of different age-groups. The method used has usually been the direct one of obtaining either the ratio of the abundance or total catch of a year-class during successive years of life, or the ratio of the relative abundance of adjacent age-groups in a sample, depending on the type of data available. Certain conditions must be satisfied, apart from adequate sampling, for this direct method to give true estimates, and it may be worth while to review briefly the theory underlying the determination of total mortality rates.

Suppose the number present of a certain year-class at the beginning of a given year X is N_X, and that a number N_{X+1} of this year-class remains at the beginning of the following year, $X + 1$. We then have the relation

$$N_{X+1} = N_X e^{-(F+M)_X}$$

where $(F + M)_X$ represents the total annual mortality coefficient during the year X. Hence

$$(F + M)_X = \log\left(\frac{N_X}{N_{X+1}}\right) \quad .. \quad .. \quad .. \quad .. \quad .. \quad (13.1)$$

Since the true abundances N_X and N_{X+1} appear in (13.1) only as a ratio, the same relationship holds for *indices* of true abundance based on the catch per unit effort. If $(F + M)$ does not vary with time or age of fish, the numbers surviving to successive years of life follow the familiar exponential trend implicit with a constant instantaneous mortality coefficient; their logarithms decrease linearly with time and have a slope equal to minus $(F + M)$.

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*Some of these suggestions have since been included in a detailed investigation of the fishing power of vessels by Mr. J. A. Gulland (1956). He has found, in particular, that there is little difference between the fishing power of trawlers belonging to the same tonnage class but of different ages and, indeed, that a closely proportional relation between relative fishing power of trawlers and gross tonnage holds over a much wider range of tonnage than is considered above.

In practice it is seldom efficient to estimate an index of instantaneous abundance as is required by (13.1), and with a continuous fishery a much better estimate is that of the mean abundance of a year-class during one year of life. Denoting this by $\bar{N}_X$ for the year X, we have by the methods of §5.2,

$$\bar{N}_X = \frac{N_X}{(F+M)_X}\left(1 - e^{-(F+M)_X}\right) \quad .. \quad .. \quad (13.2)$$

To obtain $(F + M)_X$ it is now necessary to estimate the abundance of the same year-class in the following year of life, $\bar{N}_{X+1}$. However, in the general case the total mortality coefficient will be different in year $X + 1$; denoting it by $(F + M)_{X+1}$ we have

$$\bar{N}_{X+1} = \frac{\bar{N}_X e^{-(F+M)_X}}{(F+M)_{X+1}}\left(1 - e^{-(F+M)_{X+1}}\right) \quad .. \quad .. \quad (13.3)$$

Dividing (13.2) by (13.3) gives

$$(F + M)_X = \log\left(\frac{\bar{N}_X}{\bar{N}_{X+1}}\right) + \log\left\{\frac{(F+M)_X(1 - e^{-(F+M)_{X+1}})}{(F+M)_{X+1}(1 - e^{-(F+M)_X})}\right\} \quad .. \quad (13.4)$$

so that the ratio of the mean abundance of a year-class in two successive years of life is only a true measure of the total mortality coefficient if the second logarithmic term of (13.4) is zero. This is strictly true only when $(F + M)_X = (F + M)_{X+1}$, although the error involved in neglecting the second logarithmic term is small provided the difference between $(F + M)_X$ and $(F + M)_{X+1}$ is not great, and especially if their actual magnitudes are small; in these circumstances we can put

$$(F + M)_X \simeq \log\left(\frac{\bar{N}_X}{\bar{N}_{X+1}}\right) \quad .. \quad .. \quad .. \quad .. \quad .. \quad (13.5)$$

In some fisheries and with certain types of gear it is difficult to obtain reliable indices of abundance, though adequate sampling may enable the age-composition of the annual catch to be estimated. If the annual catch of a year-class in year X is denoted by $(Y_N)_X$, and in year $X + 1$ by $(Y_N)_{X+1}$, we have instead of (13.2) and (13.3)

$$(Y_N)_X = \frac{F_X N_X}{(F+M)_X}\left(1 - e^{-(F+M)_X}\right) \quad .. \quad .. \quad .. \quad (13.6)$$

and

$$(Y_N)_{X+1} = \frac{F_{X+1} N_X e^{-(F+M)_X}}{(F+M)_{X+1}}\left(1 - e^{-(F+M)_{X+1}}\right) \quad .. \quad (13.7)$$

where F_X and F_{X+1} are values of the fishing mortality coefficient in the two years in question. Dividing (13.6) by (13.7) now gives

$$(F + M)_X = \log\left\{\frac{(Y_N)_X}{(Y_N)_{X+1}}\right\} + \log\left\{\frac{F_{X+1}(F+M)_X(1 - e^{-(F+M)_{X+1}})}{F_X(F+M)_{X+1}(1 - e^{-(F+M)_X})}\right\} \quad .. \quad (13.8)$$

It will be seen that the second logarithmic term of (13.8) contains the ratio F_{X+1}/F_X not present in (13.4). Hence estimating total mortality directly from the ratio of the catch instead of abundance of a year-class in two successive years introduces a greater error if there has been any change in fishing mortality.

The use of (13.4) or (13.5) to estimate total mortality from indices of abundance needs data for at least two successive years. Where sampling is carried out for a shorter period it is only possible to use the relative or percentage age-composition, or what Ricker (1948), following Baranov (1918), has called the "catch-curve", and mortality has to be estimated from the relative abundance of successive age-groups. The latter are of course affected by the size of the corresponding year-classes when recruited, though if fluctuations in recruitment are not too great it may be possible to estimate the order of magnitude of the total mortality from such data, as in some of the examples quoted by Ricker. In some ways a more serious problem is that of distinguishing between the effects of mortality and *trends* in recruitment, since these can be very similar, and the reader is referred to Ricker's paper for further discussion of the analysis of catch curves.

From (13.4) it is seen that errors or bias in estimates of the total mortality coefficient can arise from annual variations or changes with age in either or both the fishing and natural mortality coefficients. If the latter is the only source of variation we have an equation identical with (13.4) except that the suffixes refer to the natural mortality coefficient only. It will be seen that again a knowledge of the ratio $\bar{N}_X/\bar{N}_{X+1}$ is not sufficient to permit estimates to be obtained of the true total mortality in either year, and it is necessary to proceed by methods which allow a separation of the fishing and natural mortality rates (§14.3). Changes in F may be due either to changes in fishing effort (strictly, in the effective overall fishing intensity, see §10.2.3.1) or to changes with age in the liability of fish to capture. If temporal changes in effort occur and are known sufficiently accurately, the true total mortality can be estimated by methods based on (13.4) and described in detail in §14.3.1; indeed, far from being a disadvantage, such a situation enables the natural and fishing components of total mortality to be separated, which cannot be done from age-composition data alone if fishing effort is constant.

If F varies with age, and the gear used for sampling has the same characteristics as that used by the fleet (i.e. that which is causing the variation), estimates of the mean abundance of a year-class during successive years of life will not be comparable. It may be easy to distinguish the effects of gear selectivity and recruitment to the exploited area by means of mesh experiments and research vessel sampling, and these are likely to affect only the younger fish and perhaps over a very limited range of age. More difficult to detect might be the effects of a trend in the magnitude of F with age through 'avoidance' (see §8.1.2). The existence of such a phenomenon may result in a progressive change in the total mortality coefficient with age, but it is quite possible for the form of the trend to be such that no great differences in $(F + M)$ with increasing age are apparent. Thus the data would give a false appearance of constancy of F with age and lead to estimates of an apparently constant total mortality coefficient being obtained which would be outside its actual range of change.* Since it would usually be impossible to devise a special sampling gear which eliminated the avoidance factor, while yet providing samples comparable in all other respects to the catch of the normal gear, the only means of analysing the avoidance factor would seem to be by means of marking experiments carried out on fish of various ages (§14.1.1.3). However, it does not necessarily follow that using an estimate of an apparently constant mortality coefficient when, in fact, the true coefficient varies with age, would lead to serious errors, provided the theoretical models from which predictions are made are also based on the assumption that the mortality rate is constant. For example, in these circumstances the change in steady yield resulting from a given change in effort predicted from such a model would certainly be in the right direction and perhaps not much different from the actual change. This is an instance of the procedure we have followed with several of the problems discussed in the present part of this paper; namely, that after taking the analysis of the available data as far as possible, the simplest reasonable assumption is then made to account for the effect of any other factors that may still be present but undetectable, and the same simplifying assumption is incorporated in the population models themselves.

13.2 ESTIMATION OF THE TOTAL MORTALITY OF PLAICE AND HADDOCK

We now discuss the published age-composition data for the North Sea plaice and haddock concerning the years prior to 1939. For the plaice, Thursby-Pelham (1939, table 15) gives the catch of certain age-groups in numbers per hundred hours fishing for the years 1929-38, these data being based on Lowestoft market samples.* For the haddock we use the data of catch per ten hours fishing given by Raitt (1939, Table I) obtained by sampling from the research vessel EXPLORER, which can be rearranged in a form comparable with the plaice data. The two sets are given in Tables 13.1 and 13.2 for the plaice and haddock respectively.

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*This phenomenon can arise with small or large changes in F with age, but the likelihood that it would occur, and remain indistinguishable from sampling error, decreases as the extent of the change of F with age increases. A similar difficulty arises in the analysis of marking data where, as we shall show in §14.1.1.2, the fact that the logarithms of the numbers of marked fish recaptured in successive periods fall on a straight line need not imply that the fishing mortality rate had been constant. Further examples of the effect of trends in F with age on the age-composition of catch samples are given by Beverton and Holt (1956).

Certain facts relevant to the estimation of total mortality coefficients from these data can be stated. Thus it is known that no great variations in the total fishing effort on either population occurred during the pre-war period (see §14.3.2.2 and Appendix II) and although we cannot give any definite evidence, it is not very likely that the 'searching' factor would have been important enough to have introduced any major differences between the average and the effective overall intensity from year to year. In addition, the approximate range of age over which gear selectivity, recruitment to the exploited area, and minimum legal size limits are likely to have had an appreciable effect, can also be predicted from other data (see §§14.2 and 15.1.3). If we therefore assume that any changes in natural mortality with time are small, we can obtain approximate estimates of the total mortality coefficient by means of (13.5). Tables 13.3 and 13.4 give values of this coefficient thus obtained for each year and for each pair of age-groups.

It will be noted firstly that the apparent mortality rate is lower for the younger than for the older age-groups, becoming relatively constant only above age-groups V in plaice and II in haddock. This fact can be more easily seen by plotting the logarithms of the mean catch per unit effort of each age-group over the period of years in question against age, as shown in Figs. 13.1 and 13.2, since in both species there are sufficient data effectively to eliminate by this procedure the influence of fluctuations in recruitment. From

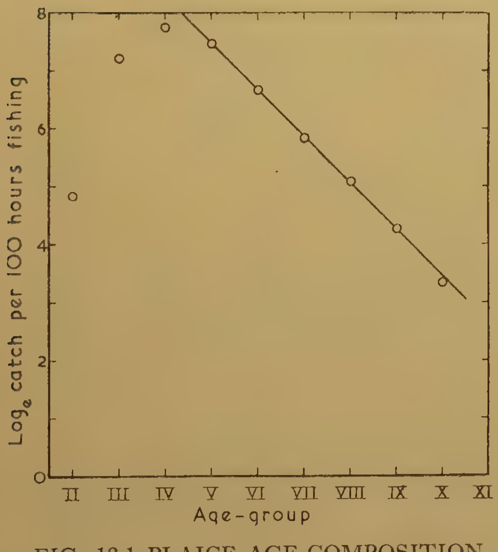

FIG. 13.1 PLAICE AGE-COMPOSITION

[Natural logarithms of the average number of each age-group caught per 100 hours fishing by 1st class steam trawlers, 1929-38; from Table 13.1. The slope of the line gives an estimate of the total mortality coefficient of $(F + M) = 0.83$.]

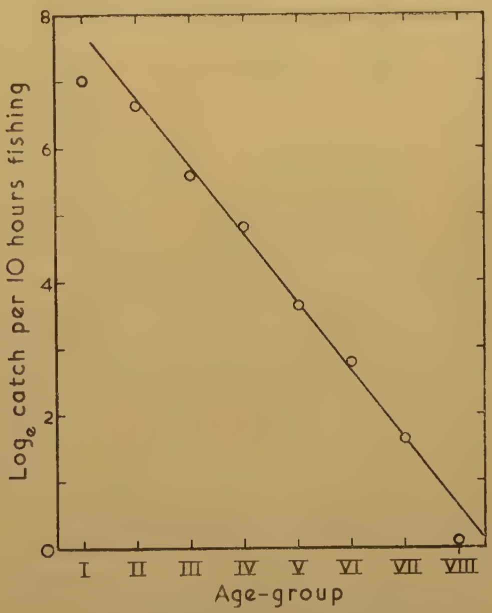

FIG. 13.2 HADDOCK AGE-COMPOSITION

[Natural logarithms of the average number of each age-group caught per 10 hours fishing by R.V. *Explorer*, 1923-38; from Table 13.2.]

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*Plaice sampling was carried out at Grimsby during some of this time, but we have not had an opportunity of analysing the data in detail for this paper. The indications are, however, that the estimates of mortality for age-groups V and above obtained from the two sources of data are of the same order of magnitude (see, e.g., Holt, 1949*b*).

a knowledge of the growth rate of each species, it seems probable that the apparently lower mortality phase in the plaice is primarily an effect of migration to the exploited area and, to a lesser extent, of rejection of undersized fish from the catch, as will be discussed further in §15.1.3. The haddock data on the other hand, were obtained by sampling the population, not the catch, so that the low mortality rate is probably real and in a general sense the phase corresponds to the selection range of the gear in use by the fleet at the time (see, however, §14.3.2.4).

We may now consider the mortality coefficients of the older age-groups which, as we have already noted, show no marked trend with age. This can be seen from the mean mortality estimates given at the bottom of Tables 13.3 and 13.4, and is of course the reason why the data of the right hand parts of Figs. 13.1 and 13.2 are fitted well by a straight line. Since we have no definite evidence to suggest that the avoidance factor is appreciable in either species, we shall use the mortality estimates from age V upwards in the plaice and age II upwards in the haddock to obtain a single value of the total mortality coefficient in each year. The next problem is therefore to decide the way in which the data should be treated so as to obtain the best estimate of the annual mortality of the population from that of its constituent age-groups. Jackson (1939) has dealt with a problem which is to some extent analogous, namely the method by which successive recaptures of marked animals may be weighted to give an estimate of the average survival rate. One of the two methods suggested, due to W. C. Stevens, is not suitable for short series of data, as Ricker (1948) has pointed out. The other, which is to use the expression

$$s = \frac{R_2 + R_3 + \ldots . + R_\lambda}{R_1 + R_2 + \ldots . + R_{\lambda - 1}}$$

where R_1, R_2 etc. are successive recaptures and s is the mean survival rate, might be adapted to the analysis of age-composition data by writing it in the form

$$e^{-(F+M)X} = \frac{{}_{\theta+1}\bar{N}_{X+1} + {}_{\theta+2}\bar{N}_{X+1} + \ldots . + {}_{\theta+\lambda}\bar{N}_{X+1}}{{}_{\theta}\bar{N}_{X} + {}_{\theta+1}\bar{N}_{X} + \ldots . + {}_{\theta+\lambda-1}\bar{N}_{X}}$$

where the prefixes denote successive age-groups, with age-group θ being the youngest of those which are free from the influence of recruitment of gear selectivity. With age-composition data, however, especially those obtained from market samples, there are several factors responsible for variation and the problem will usually be too complex to be solved by a direct weighting method such as the above. For example, there is the fact that age-determination cannot be carried out with equal accuracy on fish of all ages, and that to convert sample data to indices of abundance requires the use of other information, such as commercial statistics of yield and fishing time. Further complications arise if catches are sorted on the market into size categories, as was the case with plaice during the period covered by the data of Table 13.1. It is clear, therefore, that a solution to the problem of obtaining the best estimate of the mortality coefficient must depend on a thorough statistical analysis of the whole sampling and computing processes,* which could not be attempted while this paper was being prepared but which has since been undertaken by Gulland (1955a). For this reason we do not attempt to use other than simple arithmetic means of the mortality coefficients of each age-group to give annual estimates for the whole population, and these are presented in columns Y of Tables 13.3 and 13.4. In the haddock, where the age-composition data have not been adjusted by weighting coefficients to estimate the total catch of each age-group, we have also calculated, for comparison, estimates using Jackson's method given above. These are given in column Z of Table 13.4.

The final question to consider is whether the series of yearly mortality coefficients for each species show any trend over the course of years. They have been plotted against time and the regression lines calculated, but in neither species does the regression coefficient differ significantly from zero; this being so in the haddock for both columns Y and Z.* We shall therefore regard the years covered by the data for each species respectively as periods in which the total mortality coefficients had no trend. Consequently, we can determine mean total mortality coefficients for the years in question by taking means of the annual coefficients, these being shown at the bottom of columns Y of Tables 13.3 and 13.4. The result in each case is in close agreement with the slope of the right hand side of the curves of Figs. 13.1 and 13.2, and it will be noted that there is no appreciable difference between the values for the haddock obtained from columns Y and Z of Table 13.4. The estimates of the mean total mortality coefficients which we shall use in this paper are:—

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*See, for example, Irwin (1942).

$$(F + M) = 0.83 \text{ for plaice}^{\dagger}$$

and

$$(F + M) = 1.2 \text{ for haddock.}$$

13.3 CHOICE OF t_λ

Some of the factors relevant to deciding, in any given case, the appropriate value to take for the end of the life-span at t_λ years have already been mentioned in §3.2, and further points arise when the available data are considered. For example, we must be guided by the range of age-groups found in the samples, but the mean range in a number of samples of a population in which the abundance of successive year-classes decreases with age, must be less than that of the population itself. However, some idea of the magnitude of this discrepancy could be obtained by comparing the age ranges in samples of various sizes. Again, the process of age-determination, in many cases, becomes less certain as the age of fish increases. This, together with the fact that older fish are inevitably represented in progressively smaller numbers, renders estimates of parameters referring to them less reliable. Hence we are guided by the accuracy with which our growth and mortality curves fit the data and the extent to which they can be extrapolated beyond it.

As a final guide to the adequacy of a given value of t_λ it would be desirable to test the effect of it and other values in calculations of yield. It may, for example, be found convenient to fix a value of t_λ such that the contribution of fish of age greater than this to the yield can for practical purposes be considered negligible.

Bearing all this in mind, we use the arbitrary values

$$t_\lambda = 15 \text{ years for the plaice}$$

and

$$t_\lambda = 10 \text{ years for the haddock}$$

It will be appreciated that the concept of t_λ we have put forward does not preclude the existence of fish of greater age than the above values, and, in the case of the plaice, age-composition samples have on occasion contained fish of age greater than 15 years. The effect in each species of values of t_λ greater than the above are discussed in §17.5.2.

SECTION 14: SEPARATE ESTIMATION OF FISHING AND NATURAL MORTALITY COEFFICIENTS

The methods to be discussed in this section concern fundamentally the separation of the total mortality into its components, the fishing and natural mortality coefficients. As we have mentioned in the previous section, the detailed analysis of mortality requires certain information in addition to that obtained from age-composition data, and we have found it convenient to classify the methods of the present section according to the type of this additional data. In §14.1 is discussed the analysis of marking experiments to obtain, primarily, estimates of the absolute value of the fishing mortality coefficient, of its changes with age, and also of the constant c which relates it to the fishing intensity. Estimation of certain other parameters, such as transport coefficients, from marking data, is also mentioned. Another type of data we shall consider, in §14.2, is that of gear selection experiments, to provide estimates of the relative change of F with age. It will be appreciated that the natural mortality coefficient cannot be estimated directly, that is, we cannot count the numbers of fish that have died naturally, and M must be determined as the residue of the total mortality coefficient after F has been estimated independently and subtracted. In §14.3 we therefore return to the analysis of age-composition data and give various methods for the estimation of M from such data.

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*This conclusion is contrary to that reached by Raitt. The reason is probably that Raitt measured mortality as the percentage of I-group fish which survived to later years, but such estimates would be greatly affected by the increased mortality between age-groups I and II from 1930 onwards, which is apparent in Table 13.4. This particular mortality is ascribed by Raitt to an increase in growth rate resulting in fish becoming liable to capture at an earlier age, and we should not therefore wish it to influence estimates of total mortality as defined above. The point is discussed further in §14.3.2.4.

†The figure 0.83 for plaice was estimated graphically and differs by 0.01 from the mean given in Table 13.3; this difference is, of course, quite insignificant.

14.1 Marking Experiments: Introductory

Although our concern with marking experiments in this paper is in their application to the estimation of mortality rates rather than of the total numbers of fish in a population, nevertheless, it is this latter purpose which has hitherto received the greater attention, both in theory and practice. It is useful, therefore, to give perspective to this section by first reviewing briefly the methods available for the estimation of total numbers.

Following the classification of census methods adopted by Rasmussen and Doman (1943), it is convenient to distinguish three categories, namely (i) *enumeration*, i.e. direct counts, and therefore inapplicable to marine fish; (ii) *indices*, of which an example in marine fish is the use of pelagic egg surveys to estimate the size of the spawning stock (Buchanan-Wollaston, 1923; Simpson, 1951a); and (iii) *ratios*. This last category includes the use of marking experiments according to the methods of Schnabel (1938), Ricker (1948), Adams (1951), Schaefer (1951a) and DeLury (1951, part I), which are based on Petersen's method (variously called the 'Lincoln Index', or the 'capture-recapture' method) and Jackson's (1939) elaboration of it. It should be mentioned here that although this method has attracted considerable interest, it appears from recent publications of various authors that they are not all aware of each other's work, and it is perhaps helpful to note that the bibliographies of Bailey (1951, 1952), Schaefer (1951a), and Wohlschlag and Woodhull (1953) between them list all the publications on this subject that have come to our notice to date, except those by Howard (1948), Schaefer (1951b), Chapman (1952) and Leslie (1952). The former group review modifications of this method of population estimation and give examples of their application. This approach is, however, applicable only to confined areas within which it is possible to conduct marking experiments that ensure uniform mixing of marked and unmarked animals, or, alternatively, to cases where sampling is strictly random—which is rarely possible in practice.

The other 'ratio' methods have been developed primarily in connection with exploited populations such as fish or game. That originated by Kelker (1944) is based on the change in sex ratio of a population that is to be expected when there is differential capture of the sexes; although it has not, to our knowledge, been used in fishery investigations, there seems no reason why it should not be applicable in some situations. Actually, changes in the relative abundance of any two (or more) population sub-groups—not necessarily the sexes—which are caught in different proportions can be used, provided the size and composition of the catch are known: when these sub-groups are age-classes, the method is practically identical with what Rasmussen and Doman call census by 'kill-ratios', which is in effect that used in the present paper.* If predation by man is the only cause of a fairly high mortality, then a knowledge of the catch and of the way in which the population declines gives immediately an estimate of the initial population (see, e.g. Moran, 1951), and DeLury

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*Chapman, D. G. (1955) has recently published a general study of the method of "Population estimation based on change of composition caused by selective removal;" to which the interested reader is referred.

(1951, part III) has discussed how in other circumstances catch data and marking experiments may be combined for the same purpose. In general, if an estimate of the total number in a large exploited fish population is required, it can conveniently be obtained from a knowledge of the mortality rates and the total catch, as discussed in §15.2.1.

Certain contributions to the problem of determining population parameters by means of marking experiments have recently been published, notably those by Leslie and Chitty (1951) and Moran (1952), dealing with estimation of death-rates, but for the most part these are not immediately relevant to the study of exploited fish populations since they are primarily concerned with populations in which there is only one cause of mortality and in which marked and unmarked individuals behave identically. The importance in the present connection of the papers quoted lies in the statistical treatment of recapture data, which is considered in much greater detail than we have attempted.* Early fishery workers used marking experiments to obtain an under-estimate of the true fishing mortality coefficient, and did not attempt to do more than state that the true fishing rate must have been greater than the rate of recapture of marked fish, owing to loss of marks and other causes. In later years, Thompson and Herrington (1930), Graham (1938a) and Ricker (1948), have put forward methods of analysis the purposes of which are to provide unbiased estimates of the true fishing coefficient, that is, estimates that are free from the influence of other losses. Now, the main object of a marking experiment is to set up, and examine the properties of, an 'experimental' population of marked fish in which certain parameters, that would be difficult or impossible to estimate in the 'natural' population, can be determined with some accuracy. As might be expected, therefore, certain of the principles and methods on which have been based the theoretical models in the first two parts of this paper are applicable also to the analysis of marking experiments, and during the investigation to be described in this section it was found necessary to re-examine the methods of these authors and to extend them to deal with some of the complications that arise when detailed analysis is attempted.

We have found it convenient to discuss first the methods which aim at providing estimates of the fishing mortality coefficient (§14.1.1) and then to proceed to methods for analysing the effects of some of the factors other than fishing that are responsible for the loss of marks (§14.1.2). Finally, in §14.1.3, we illustrate their application by means of an analysis of part of the data obtained from the post-war plaice marking experiments in the North Sea, and in so doing obtain provisional estimates of certain parameters for use later in this paper.

14.1.1. *Estimation of the fishing mortality coefficient*, *F*

The general type of marking experiment with which we are primarily concerned is that in which a known number of marked fish are released in one batch, and recaptures are summed over known periods of time. This is the situation dealt with specifically by Thompson and Herrington, and by Graham,† and corresponds closely to that discussed by Ricker (1948, page 60) of a marking experiment extending over more than one year, marking being done just before the first fishing season.

14.1.1.1 *Fishing intensity constant; comparison with methods of Thompson and Herrington, and Graham*

The simplest assumption we can make is that the subsequent reduction of a given initial number of marked fish procedes at a constant relative rate. The instantaneous coefficient describing this reduction can be considered as the sum of a number of components which can be grouped into: (a) that relating to fishing, and (b) those relating to other causes, including, specifically, natural mortality, marking mortality, the accidental detachment of marks from living fish, and the failure of fishermen to return captured marks.

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*See also Gulland (1955 b), who deduces maximum likelihood estimates for fishing and natural mortality from recapture data.

†Graham used data as published by Borley (1916), in which recaptures from a number of separate liberations spread over several years were arranged according to their duration of liberty. This arrangement produced results which Graham treated as if the data came from one large experiment carried out instantaneously, but with the advantage that fishing and other loss rates were in effect averaged over a period of time. This procedure is examined further in §§14.1.1.1 and 14.1.1.2.

This assumption also serves to illustrate the general methods we shall be using, and to analyse those of the above authors.

If we denote the coefficient of reduction of marks due to fishing by F, and that of the sum of all other causes by X, then the total rate of reduction of marks, with F and X assumed constant, can be represented by the equation

$$\frac{dN}{dt} = -\left(F + X\right)N$$

where N is the number of marked fish remaining at any time t. Hence, on solving, we have

$$N_t = N_0 e^{-(F + X)t}$$

where N_0 is the initial number of marked fish liberated. The rate of recapture of marks at this time is therefore

$$\frac{dn}{dt} = FN_t = FN_0 e^{-(F + X)t}$$

and the number recaptured during the period $t = t_0$ to $t = t_1$ is given by the equation

$$n_1 = \frac{FN_0}{F + X}\left(1 - e^{-(F + X)(t_1 - t_0)}\right) \quad \ldots \quad \ldots \quad (14.1)$$

and, similarly, from t_1 to t_2, by

$$n_2 = \frac{FN_0 e^{-(F + X)(t_1 - t_0)}}{F + X}\left(1 - e^{-(F + X)(t_2 - t_1)}\right) \quad \ldots \quad (14.2)$$

If equal periods of time are considered, so that

$$t_1 - t_0 = t_2 - t_1 = \tau \text{ (say)}$$

then the rth term of the series

$$n_1, n_2, \ldots \text{ etc. } \ldots n_r \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.3)$$

becomes

$$n_r = \frac{FN_0 e^{-(F + X)(r - 1)\tau}}{F + X}\left(1 - e^{-(F + X)\tau}\right) \quad \ldots \quad \ldots \quad (14.4)$$

It will thus be seen that each term contains two unknowns, viz.: F and X, assuming that the initial number of marked fish, N_0, is known. The methods of Thompson and Herrington (1930) and of Graham (1938a) involve the manipulation of this series, or a derivative of it, with the purpose of eliminating the other loss rate X, and we now consider them in more detail.

Thompson and Herrington wished to obtain a value for the 'fishing rate', defined as the proportion of the initial number of marks liberated which would be recaptured during a given period after liberation if no other cause of reduction of number of marked fish had been operating. In our terminology, and denoting by n' the number thus recaptured in time τ, we find that Thompson and Herrington's 'fishing rate' is defined by the ratio

$$\frac{n'}{\tau N_0} = 1 - e^{-F\tau} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.5)$$

since X is now zero by definition. Graham, on the other hand, by taking τ as small as possible, used the ratio $n'/\tau N_0$ as a measure of the 'instantaneous fishing rate,' the latter being equivalent to the fishing mortality coefficient, F, as we have defined it in this paper. It will be seen that for small enough values of the product $F\tau$, the two definitions become identical, since

$$1 - e^{-F\tau} \rightarrow F\tau$$

as

$$F\tau \rightarrow 0.$$

The methods of both authors are based on the proposition that series (14.3) or a derivative, when extrapolated back to zero time, i.e. the moment of liberation, would provide an estimate of n', since only at this moment are non-existent the 'other losses' which render actual recaptures n_1, n_2, n_3, etc. unusable. We must now examine the consequences of this extrapolation.

Basically, Graham's method is to extrapolate series (14.3) (which is a geometric series with constant ratio $e^{-(F+X)\tau}$) back to time zero; in other words, to estimate the hypothetical term $r = 0$ from a knowledge of the terms $r = 1, 2, \ldots.$ etc. Putting $r = 0$ in (14.4) we find

$$n_0 = \frac{FN_0}{F + X}\left(e^{(F+X)\tau} - 1\right)$$

so that the instantaneous fishing rate as defined by Graham, becomes

$$\frac{n_0}{\tau N_0} = \frac{F}{(F + X)\tau}\left(e^{(F+X)\tau} - 1\right) \quad \ldots \quad \ldots \quad \ldots \quad (14.6)$$

It will be seen that this procedure has not had the desired effect, namely to eliminate the other-losses, since (14.6) still contains the other-loss coefficient X. Consequently, the estimate of the fishing rate is not free from the influence of other-losses and, moreover, (14.6) does not give a good approximation to the instantaneous coefficient F unless τ is very small. For example, with the values

$$F = 1.0$$

$$X = 1.5$$

$$\tau = 0.25 \text{ years}$$

where F and X are of the order of magnitude found by Graham, (14.6) results in the estimate

$$\frac{n_0}{\tau N_0} = 1.4$$

or a 40% overestimate of the true value of F; if the method had been used to analyse recapture data summed in yearly intervals with the same values of F and X (i.e. if $\tau = 1.0$) we find

$$\frac{n_0}{\tau N_0} \simeq 5$$

so that very large errors would have been introduced.

Now Borley's data, to which Graham applied his method, had the peculiarity that all recaptures within the three-month period of liberation had been discarded, and Graham made allowance for this by taking zero time as $1\frac{1}{2}$ months following the commencement of liberation, i.e. he estimated, in effect, the term $r = \frac{1}{2}$ instead of $r = 0$. There is no exact way of correcting for discarded returns, unless it is possible to use methods such as (14.27) or (14.33) which do not require a knowledge of the initial numbers of marks liberated, and Graham's procedure is as good as any. It is interesting, however, to see what errors are involved by back-extrapolating to $r = \frac{1}{2}$ with data in which it can be supposed that liberation is effectively instantaneous and no recaptures are discarded. Thus putting $r = \frac{1}{2}$

in (14.4) we find

$$n_{\frac{1}{2}} = \frac{FN_0 e^{(F+X)(\tau/2)}}{F+X}\left(1 - e^{-(F+X)\tau}\right)$$

$$= \frac{2FN_0}{F+X}\sinh\left(F+X\right)\frac{\tau}{2}$$

so that Graham's instantaneous fishing rate is

$$\frac{n_{\frac{1}{2}}}{\tau N_0} = \frac{2F}{\tau\,(F+X)}\sinh\left(F+X\right)\frac{\tau}{2} \quad \ldots \quad \ldots \quad \ldots \quad (14.7)$$

Again we find that back-extrapolation has not eliminated X, but the property of the hyperbolic sine is such that as the quantity $(F + X)(\tau/2)$ becomes smaller

$$\sinh\left(F+X\right)\frac{\tau}{2} \to \left(F+X\right)\frac{\tau}{2}$$

so that

$$\frac{2F}{\tau\,(F+X)}\sinh\left(F+X\right)\frac{\tau}{2} \simeq F$$

and this approximation is useful over a wider range of values of F, X and τ than is the case with (14.6). Table 14.1 gives values of the function (14.7) for selected values of F, X and τ, these covering a range which could reasonably be expected to be encountered in practice. It is found that with $\tau = 0.1$ the value of (14.7) is very close to the true instantaneous coefficient, F, so that the method is a useful one for obtaining a rapid estimate of this quantity provided recaptures can be summed in small fractions of a year and it is possible to regard the fishing mortality coefficient as effectively constant over the period during which recaptures are obtained. Applying the methods developed in the following section to the data used by Graham indicates that the value of X was unlikely to have been greater than 2.0, so that with $\tau = 0.25$ years the estimate of F obtained by Graham by back-extrapolating to $r = \frac{1}{2}$ (i.e. $F = 0.74$) is unlikely to be more than about 10% higher than the true value. Graham's estimate agrees well, in fact, with those we find in §§14.3.2.1 and 14.3.2.2.

Thompson and Herrington's procedure differs from that of Graham in that they first converted series (14.3) into a form in which each term represents the ratio of the number of marks returned during a period to the number unaccounted for up to the beginning of that period. Expressing the resulting series in our terminology it becomes

$$\frac{n_1}{N_0}, \frac{n_2}{N_0 - n_1}, \frac{n_3}{N_0 - (n_1 + n_2)}, \ldots \text{etc.} \ldots \frac{n_r}{N_0 - \sum_{x=0}^{r-1} n_x} \quad \ldots \quad \ldots \quad (14.8)$$

where n_0 is taken to be zero. To discuss the properties of this series we again need to express the rth term as a function of the coefficients F and X, but only the summation term in the denominator presents any difficulties in this connection. The summation term

$$\sum_{x=0}^{r-1} n_x$$

expresses the total recaptures between time t_0 and time $t_0 + (r - 1)\tau$. This is also given by the integral

$$FN_0\int_0^{(r-1)\tau} e^{-(F+X)t}\,dt$$

so that

$$\sum_{x=0}^{r-1} n_x = \frac{FN_0}{F+X}\left(1 - e^{-(F+X)(r-1)\tau}\right) \qquad \ldots \quad \ldots \quad (14.9)$$

The rth term of series (14.8) is therefore

$$\frac{1 - e^{-(F+X)\tau}}{1 + \frac{X}{F}e^{(F+X)(r-1)\tau}} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.10)$$

Ricker, (1948, page 74), in analysing the properties of this series derived the general term corresponding to (14.10) but without taking the preliminary step of resolving the summation term. He was consequently led to the conclusion that the series was discontinuous between the second and third terms, which is not the case. Unlike the original series (14.3) however, Thompson and Herrington's modified series is not geometric, as can be demonstrated algebraically from the general term (14.10), and this fact invalidates their procedure of fitting a linear regression to the logarithms of successive terms. Ricker detected this property by trial computations and showed that the logarithms of successive terms of series (14.8) when plotted give a curve convex upwards, though the curvature is only pronounced between the origin and the 1st term, and would therefore be difficult to detect from data when, of course, the origin is unknown. Consequently, the logarithms of successive terms of Thompson and Herrington's series do not lie on a straight line, and cannot therefore be extrapolated back linearly. The series can, however, be reduced to a linear form in the following way. From (14.10) we have

$$\log\left(\frac{1 - e^{-(F+X)\tau}}{r\text{th term}} - 1\right) = (F + X)(r - 1)\,\tau + \log\left(\frac{X}{F}\right) \quad \ldots \quad (14.11)$$

This is a linear equation in r, which could be fitted to the weighted observations by least squares, and an estimate made of the term at zero time, viz.

$$\frac{1 - e^{-(F+X)\tau}}{1 + \frac{X}{F}e^{-(F+X)\tau}} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.12)$$

It will be seen that this is still not the quantity that Thompson and Herrington were seeking, the value of (14.12) depending as much on the value of X as of F, and consequently an error is introduced in using it as an estimate of $1 - e^{-F\tau}$. Moreover, (14.12) is itself incorrectly estimated by linearly extrapolating the logarithms of series (14.8) to zero time, and thus a further error is introduced which may, for certain values of F and X, be additive with the first.

The fact that two sources of error are present in Thompson and Herrington's method makes it difficult to produce a short table comparable to Table 14.1, but we can use their data to give an example of the error involved in estimating F. If we assume, as did the authors, that in their case F and X were constants, (14.15) and (14.16) derived below give true solutions for F and X, and it is only necessary to know two successive recaptures. Thus plotting the logarithms of the successive recaptures from the 1925 liberations given by Thompson and Herrington showed them to be fitted well by a straight line, with the first two falling almost exactly on it. Taking these, viz.: 273 and 113, as the best estimates of n_1 and n_2 respectively, and with $N_0 = 1462$ and $\tau = 1$ year, we find that

$$F = 0.28$$

$$\text{and } X = 0.60$$

Hence we can compute the quantity $1 - e^{-F\tau}$, i.e. the fishing rate $n'/\tau N_0$ as defined by these authors, and we have

$$1 - e^{-F\tau} = 0.245$$

Now the true value of the zero term of Thompson and Herrington's series can be calculated from (14.12) using the above values of F and X, and is found to be 0.311. If this value is taken as an estimate of the quantity $n'/\tau N_0$ it gives the value

$$F = 0.372$$

to be compared with the true value of 0.28. However, owing to the curvilinear property of the logarithms of series (14.8), Thompson and Herrington's linear back-extrapolation method gave the estimate

$$\frac{n'}{\tau N_0} = 0.404$$

which is equivalent to $F = 0.518$ (see Thompson and Herrington, figure 20).

The conclusion we wish to emphasize is that both the methods of back-extrapolation discussed above lead to immediate discrepancies within the assumptions made, usually small in the case of Graham's method, but possibly large with that of Thompson and Herrington; thus the estimate of the fishing mortality coefficient obtained by the latter authors may have been up to twice as large as the true value.

Since the principle of back-extrapolation does not achieve the object desired, which is to eliminate the 'other-loss' rate X from the estimate of F, we must proceed by other methods which are similar in principle to those used by Ricker (1948). The equations for recaptures, viz. (14.1) and (14.2), suggest how rigorous solutions for F and X may be obtained. Dividing (14.2) by (14.1) we have

$$\frac{n_2}{n_1} = e^{-(F+X)\tau} \quad \ldots \quad (14.13)$$

so that

$$F + X = \frac{1}{\tau}\log\left(\frac{n_1}{n_2}\right) \quad \ldots \quad (14.14)$$

Substituting (14.13) and (14.14) in (14.1) gives

$$F = \frac{\dfrac{n_1}{\tau}\log\left(\dfrac{n_1}{n_2}\right)}{N_0\left(1 - \dfrac{n_2}{n_1}\right)} \quad \ldots \quad (14.15)$$

Hence, from (14.14),

$$X = \frac{1}{\tau}\left\{\log\left(\frac{n_1}{n_2}\right)\right\}\left\{1 - \frac{n_1}{N_0\left(1 - \dfrac{n_2}{n_1}\right)}\right\} \quad \ldots \quad (14.16)$$

If successive numbers of recaptures n_1, n_2, n_3 . . . . etc., are available, a linear regression may be fitted to their logarithms plotted against time, weighted by an expression such as that given by Jackson (1939). If time zero is taken at the point on the time axis corresponding to n_1, then in the regression equation

$$y = a + bx$$

a is an estimate of $\log n_1$, and b of $1/\tau \log (n_1/n_2)$, $(= F + X)$, in (14.15) and (14.16) above, so that F and X may be determined from these equations as before. Ricker discusses this case in some detail and arrives at a similar solution for F and X, though it should be noted that the procedure of fitting a straight line to the logarithms of recaptures is not entirely satisfactory, since successive values are not statistically independent. A method based on maximum likelihood estimation is reasonably simple to derive and calculate when there is only one cause of mortality, and also provides standard errors of estimation, but extension to the more complex cases that frequently arise in practice presents many difficulties (Moran, 1951, and see also DeLury, 1951, Pt. II). On the other hand, a preliminary graphical treatment permits a critical examination of any trends or irregularities that there may be in the data, thus allowing any serious departure from the simple assumptions on which the theory is based to be detected; moreover, fitting lines by eye or by some standard method so that repetition is possible, is probably satisfactory for our purposes.

Before leaving the simple case of F and X constant, we must consider the problem of combining the data from a number of separate liberations. One possibility, which may sometimes be desirable, is to determine separate estimates of F and X from each batch of liberations, but the problem then arises of how the various estimates should be weighted to produce the best combined estimates. This difficulty is avoided by the procedure used by Graham (1938), in which the recaptures from the individual batches are arranged according to their duration of liberty and then summed. Let us suppose that in a marking experiment fish are liberated in a number of batches a, b, ... etc. . . . . z, the numbers liberated being ${}_aN_0$, ${}_bN_0$, ... etc. . . . . ${}_zN_0$. The recaptures during the rth period following the liberation of ${}_iN_0$ fish in the ith batch can then be written as

$$ {}_in_r = \frac{{}_iN_0\, e^{-(F+X)(r-1)\tau}}{F+X}\left(1 - e^{-(F+X)\tau}\right) $$

The total recaptures obtained during the rth periods following all liberations are therefore

$$ \sum_{i=a}^{z} {}_in_r = \frac{e^{-(F+X)(r-1)\tau}}{F+X}\left(1 - e^{-(F+X)\tau}\right)\sum_{i=a}^{z} {}_iN_0 \quad \ldots \qquad \ldots \quad (14.17) $$

This equation is exactly analogous in form to (14.4), and shows that the summed liberations and recaptures can be used to estimate F and X by the same procedure as discussed above in connection with (14.15) and (14.16). That this method can be used is due to the fact that the ratio of recaptures to liberations in any given period is the same for all batches; the summed recaptures are therefore the same ratio to the summed liberations, as can be seen from (14.17). The method is therefore strictly valid only if F is constant and X can be assumed to be so, and the modifications required when F varies with time will be discussed in the following section. It is, nevertheless, a useful procedure to adopt when the fishing intensity is unknown, since though it does not eliminate the effects of variation in intensity it reduces them considerably (see §14.1.1.2).

14.1.1.2 *Fishing intensity varying with time*

While it may often be possible to find a period of sufficient length subsequent to the liberation of a number of marked fish during which the value of F may be regarded as effectively constant, in general the fishing intensity, and hence F, will vary with time. If this variation with time can be determined, for example from commercial statistics of effort converted to standard units of fishing intensity (see §12), then the problem can be dealt with theoretically.

The possibilities of treating F as a continuous function of time, even though this may be known from the data, are limited by the mathematical complexities involved. The simplest continuous function of intensity with time that is likely to be of use in practice is the linear form, which leads to expressions for recaptures in given periods of time analogous to those developed in §8.1. These can be solved graphically to give estimates of F and X, but a more flexible method in practice is to treat fishing intensity as a discontinuous function of time, as Ricker (1948, p. 82) has done, and to divide the duration of the marking experiment into a number of shorter periods during each of which the intensity is assumed constant but changing abruptly from one period to the next.

It is now desirable to consider the more general case in which the recapture periods are of unequal duration, since if the fishing intensity varies appreciably it might be advantageous to choose the length of the recapture periods such that very small numbers of recaptures in any one period are avoided. We shall therefore suppose that the time following the liberation of N_0 marked fish is divided into periods of length $\tau_1, \tau_2, \ldots . \tau_r \ldots .$ etc., during which the fishing intensity is $f_1, f_2, \ldots . f_r$, etc. Since we have

$$F_r = cf_r$$

where F_r is the fishing mortality coefficient during the rth period, the number recaptured during the rth period is given by the previous methods as

$$n_r = \frac{cf_r\,N_0 e^{-\sum\limits_{p=0}^{r-1}(cf_p + X)\tau_p}}{cf_r + X}\left(1 - e^{-(cf_r + X)\tau_r}\right) \quad \ldots \quad \ldots \quad (14.18)$$

(compare (14.4))

in which τ_0 is taken as zero. Dividing n_{r+1} by n_r gives

$$\frac{n_{r+1}}{n_r} = \frac{f_{r+1}}{f_r}\left\{\frac{(cf_r + X)(1 - e^{-(cf_{r+1} + X)\tau_{r+1}})}{(cf_{r+1} + X)(1 - e^{-(cf_r + X)\tau_r})}\right\} e^{-(cf_r + X)\tau}$$

Rearranging and taking logarithms gives the expression

$$\frac{1}{\tau_r}\left[\log\left(\frac{n_r\,f_{r+1}}{n_{r+1}\,f_r}\right) + \log\left\{\frac{(cf_r + X)(1 - e^{-(cf_{r+1} + X)\tau_{r+1}})}{(cf_{r+1} + X)(1 - e^{-(cf_r + X)\tau_r})}\right\}\right] = cf_r + X \quad \ldots \quad (14.19)$$

(compare (13.4))

The unknown parameters in this expression are c and X, and to obtain solutions for them we may as a first step put the second logarithmic term to zero, thus obtaining

$$\frac{1}{\tau_r}\log\left(\frac{n_r\,f_{r+1}}{n_{r+1}\,f_r}\right) = cf_r + X$$

This expression is linear in f_r, so that by plotting the left hand side against f_r we obtain a straight line of which the slope and intersect give first estimates of c and X respectively. Inserting these values in the left hand side of (14.19) and plotting now the whole of it against f_r enables another straight line to be fitted which gives more exact estimates of c and X. The process can be repeated until successive plots of (14.19) give no improvement in the fit to a straight line, continuation depending on the extent to which f_r differs from f_{r+1}. In practice it is seldom necessary to continue beyond the third approximation. It will be seen that a minimum of three recapture periods is required to obtain solutions for both c and X from (14.19); if only two are available we must use in addition the total number of liberations N_0 in the equation

$$n_1 = \frac{cf_1\,N_0}{cf_1 + X}\left(1 - e^{-(cf_1 + X)\tau_1}\right) \quad \ldots \quad \ldots \quad \ldots \quad (14.20)$$

to separate the coefficients (compare (14.1)), having estimated their sum from (14.19). This technique is applied in §14.1.3.1. When c has been determined with sufficient accuracy the fishing mortality coefficient in any period can be computed directly by multiplying c by the appropriate fishing intensity.

It will be noted that the above method is approximate to the extent that the change in fishing intensity is assumed to be discontinuous, whereas in practice it is likely to be continuous; it is therefore important to establish that no appreciable bias will be introduced by using this method. For this purpose we have taken the case of a fishing intensity decreasing linearly throughout the experiment, and calculated the theoretical number of recaptures from the exact equation for a linear change in intensity. These recaptures were used to estimate c and X from (14.19), and then compared with the true values. Defining the change in fishing intensity by the equation

$$f_t = a - bt$$

the fishing mortality coefficient as a function of time is given by the equation

$$F_t = c\,(a - bt)$$

Taking, for simplicity, all recapture periods to be of the same duration τ, the general equation for the recaptures during the rth period is given by methods analogous to those developed in §8.1 as

$$n_r = N_0 e^{-\left\{(ca+X)(r-1)\tau - \frac{1}{2}cb\tau^2(r-1)^2\right\}}\left\{1 - e^{(H_{r+1}^2 - H_r^2)} - Xe^{-H_r^2}\sqrt{\frac{2}{cb}}\int_{H_r}^{H_{r+1}} e^{+Z^2}\,dZ\right\}$$

where

$$H_r = -\frac{ca+X}{\sqrt{2cb}} + (r-1)\tau\sqrt{\frac{cb}{2}}$$

To compute values of n_r from this equation we have used the values

$$N_0 = 1000$$

$$c = 1$$

$$X = 0.5$$

$$\tau = 1 \text{ year}$$

$$a = 1.1625$$

$$b = 0.325$$

thus obtaining the first three values of n_r as $n_1 = 523$, $n_2 = 90$ and $n_3 = 17$. If we now regard the change in intensity as discontinuous we should determine the mean intensities in each of the first three recapture periods; these were $f_1 = 1.0$, $f_2 = 0.675$ and $f_3 = 0.35$. Using these values, and those of the theoretical recaptures given above, in (14.19) and solving iteratively, gave the final estimates

$$c = 1.035$$

$$X = 0.461$$

which are very similar to the true values. In practice, of course, sampling variation of recaptures would introduce greater errors in c and X than the method itself, quite apart from the fact that the trend in fishing intensity could probably not be estimated with great accuracy. The example we took involved an appreciable trend in intensity and a relatively long recapture period, and for both these reasons was a fair test of the accuracy of the method. Thus we can conclude that the simplification of treating changes in intensity as discontinuous is unlikely to involve appreciable bias.

Now the logarithms of the theoretical recaptures listed above were found to lie almost exactly on a straight line—and certainly their trend would be indistinguishable from linearity when observational error is taken into account. If nothing were known about the trend in the fishing intensity, it might seem reasonable to regard such recaptures as being generated by a constant intensity, and to estimate F and X from them by means of (14.15) and (14.16), since in these circumstances also the logarithms of successive recaptures would be linear. If this is done, however, we obtain the estimates

$$F = 1.10$$

$$X = 0.62$$

This value of X is not greatly different from the true value, but that of F is outside the range of trend and is nearly twice the mean value of F during the period of the experiment. The reason for this is, of course, that a rapid decrease in the numbers of successive recaptures would imply—if the fishing intensity was really constant—a rapid depletion in the number of surviving marked fish, and hence a high fishing mortality rate; the true cause of the rapid decrease in numbers of recaptures is that the fishing intensity is itself declining. If the trend in intensity is upwards the value of F obtained in this way would be below the range of values of that coefficient. This example serves to emphasize the desirability of obtaining information on possible changes in fishing intensity before using the returns of marked fish to compute estimates of F and X. The presence of a linear trend in the logarithms of successive recaptures is no criterion of the constancy of F, or for that matter of X.* A wide range of roughly linear trends in intensity could result in the logarithms of recaptures being fitted adequately by a straight line when sampling variation is taken into account, and the bias caused by computing F and X on the assumption that the intensity is constant may well be serious, as in the above example.

We must now discuss the adaptation of the above method necessary to combine data from a number of separate liberations. With the same terminology as in §14.1.1.1, the recaptures during the rth period following the liberation of the ith batch of marked fish can be written as

$$_{i}n_{r} = \frac{c\,_{i}f_{r}\,_{i}N_{0}e^{-\sum\limits_{p=0}^{r-1}(c\,_{i}f_{p}+X)\tau}}{c\,_{i}f_{r}+X}\left(1 - e^{-(c\,_{i}f_{r}+X)\tau}\right)$$

in which $_{i}f_{r}$ denotes the fishing intensity during the rth period of the ith liberation, the duration of all recapture periods being taken as constant for all batches and equal to τ. Note that the ratio $_{i}n_{r}/_{i}N_{0}$ is now different for each batch, because its value depends on that of $_{i}f_{r}$; therefore we cannot simply sum all recaptures and liberations and proceed as if the latter were simultaneous, as is possible when F is constant. Consider, however, the situation during the rth periods following the liberation of each batch. At the beginning of each rth period there will be a certain unknown density of marked fish surviving from the batch in question, but during the course of the rth periods known numbers of recaptures will be obtained as the result of fishing intensities of various but known magnitudes. This situation is exactly analogous to that arising in §10.2.3.1 when discussing the case in which the density of fish and the fishing intensity vary spatially, and we can similarly define an *effective constant fishing intensity*, f_{r}', such that if it applied in the rth periods following all the separate liberations, it would produce the same total number of recaptures as that actually observed. Thus f_r' can be evaluated from an expression analogous to (10.30),* i.e.

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*See also DeLury (1951, p. 294).

$$f_r' = \frac{\sum_{i=a}^{z} {}_in_r}{\sum_{i=a}^{z} \frac{{}_in_r}{{}_if_r}} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.21)$$

and the expression for the total recaptures during all the rth periods, analogous to (14.17), is

$$\sum_{i=a}^{z} {}_in_r = \frac{cf_r' e^{-\sum_{p=0}^{r-1}(cf_p'+X)\tau}}{cf_r'+X}\left(1 - e^{-(cf_r'+X)\tau}\right)\sum_{i=a}^{z} {}_iN_0 \quad \ldots \quad \ldots \quad (14.22)$$

In (14.22) it is seen that the ratio

$$\frac{\sum_{i=a}^{z} {}_in_r}{\sum_{i=a}^{z} {}_iN_0}$$

is independent of i, so that by computing values of f_r' from (14.21) it is possible to use summed recaptures and liberations in (14.19) to estimate c and X.

An important feature of these methods based on the case in which fishing intensity varies in time is that it is not necessary to know the number of marked fish liberated to obtain estimates of F and X. This can be seen from (14.19) in which N_0 does not appear. Estimates can therefore be obtained free from bias due to any mortality of marked fish that may occur within a short time of the marking operation, as is discussed further in §14.1.2.1.

Finally, a special case of the temporal variation of fishing intensity should be noted. It may happen that the fishing intensity remains sufficiently steady following the liberation of two or more batches of marked fish for the total loss rate $(F + X)$ to be estimated for each batch by means of (14.14). If, however, the magnitude of the fishing intensity is different for each batch of liberations and recaptures, but it is permissible to assume that the 'other-loss' rate X is the same for each, the estimates of $(F + X)$ obtained from the various batches should be linearly related to the corresponding fishing intensities. Thus for the ith batch of liberations and recaptures, when the fishing intensity was f_i, we have

$$(F + X)_i = cf_i + X$$

and solutions for c and X can be obtained directly from the slope and intercept of the regression of $(F + X)_i$ on f_i without iteration and without using the number of fish liberated.

The above procedure is exactly similar to that described and exemplified in §14.3.2.2 for obtaining separate estimates of F and M from age-composition data. In both cases it is necessary to assume that the components of total mortality other than fishing are constant. With age-composition data, the component other than fishing is the true natural mortality, which in heavily fished populations may often be small relative to F. In the case of marking experiments the parallel assumption that the other-loss rate X is the same for several different batches of liberations is much less satisfactory, if only because it may be at least as large as F and possibly much larger (see, e.g., §14.1.3.1), so that relatively small variations in its magnitude can introduce serious errors in the estimate of F. Nevertheless, the above method of treating recapture data is worth attempting when the requirements appear to be satisfied, especially when a number of batches can be so treated and a good regression can be obtained.

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*With spatial variation in intensity, the catches from each sub-area are obtained simultaneously, whereas in the present case this is not so. It will be realised, however, that the time factor does not enter in this form into the definition of either $\bar{f}$ or f', and both quantities are weighted mean intensities, the weighting coefficients being the same in each case, i.e. the density of fish corresponding to the individual intensities.

14.1.1.3 *Fishing mortality varying with size and hence age of fish*

The problem of fishing mortality varying with the size, and hence age, of fish can conveniently be considered at this point. The possible significance of a variation of this sort could be investigated, as Ricker (1948) suggests, by comparing the percentage recaptures of marked fish of different size groups over a given period. If these showed appreciable differences, then it would be necessary to treat each size group of marked fish as an independent marked population, and any of the methods described here could be used to provide estimates of F and X for each size group. If the length of period over which recaptures were summed was such that growth was negligible in comparison with the magnitude of the size-class interval, it would be possible to obtain F as a function of age of fish over a mesh selection range and hence to determine the mean selection point, and also to detect in the higher age-groups the occurrence of 'avoidance' and thus obtain the appropriate function for use in equations of type (8.10). Where a mesh regulation is in force this procedure offers a means of testing whether the selection of the commercial gear is that which would be expected if the specified size of mesh were actually in use by the fleet (see §19.2.1.2). Comparison of results with those obtained from mesh selection experiments might show the existence of differential liability to capture of marked and unmarked fish of the same size (see §14.1.1.6). It may also be possible to obtain an indication of any variation of X with age by this means.

14.1.1.4 *Fishing intensity varying spatially*

We now consider the case of fishing intensity varying spatially, with X assumed constant (i.e. independently of time and location) as before. This is an aspect of the analysis of marking experiments likely to be important in all but small water basins, but as far as we know has not been treated in detail hitherto. The general problems raised by a non-uniformly distributed fishing effort have been discussed in §10.2; with a marking experiment conducted in such an area, the same concepts and theoretical methods are applicable.

There are two main ways of estimating the fishing mortality by marking experiments in a large area in which the effort is not distributed uniformly. The simplest approach from the theoretical point of view is to determine directly the effective overall fishing mortality coefficient (as defined in §10.2.3.1), by releasing marked fish over the whole area in proportion to the population density at each point. In practice, this would amount to marking all fish caught by a research vessel fishing with uniform intensity over the whole area and liberating them at the place of capture. The recaptures could then be used to compute estimates of $\tilde{F}$ and X by the methods described previously, using estimates of the effective overall intensity, $\tilde{f}$, as defined by (10.30) if this is found to vary with time. The value of $\tilde{F}$ thus estimated could be compared directly with the total mortality coefficient obtained from the age-composition of the catch to give an estimate of the natural mortality coefficient M (see §14.3.2.1). There are, however, likely to be considerable practical difficulties if the exploited area is at all large. It would be impossible to cover an exploited area the size, for example, of the Southern North Sea in a reasonable time, with a single research vessel. Yet unless liberation is completed within a short time (in theory, the liberation must be instantaneous) the theoretical simplicity of the method is lost and marking by density has no special advantages, because by the time the liberation is completed the ratio of marked to unmarked fish is unlikely to be the same over the whole area. Moreover, liberation must not be restricted to regions of highest density and commercial fishing intensity, because if so, the research vessel's time is not used to the best advantage.

The other approach is not to attempt to estimate the effective overall coefficient directly, but to determine the relationship between fishing intensity and the fishing mortality coefficient generated by it—i.e. to estimate the constant c—in a part only of the exploited area; the effective overall fishing mortality coefficient can then be computed from (10.28) by means of commercial statistics of catch and effort for the whole exploited area. This is the general principle that has been followed in the design of the English post-war marking experiments on North Sea plaice, discussed in §14.1.3. There are several variations of this method, each having certain advantages and disadvantages, practical and theoretical; since their suitability depends largely on the characteristics of the fishery in question, it is necessary to give some attention to each.

One procedure is to restrict liberation of marked fish to a part of the exploited area which is small enough for the fishing effort and the marked fish to be treated as uniformly distributed within it. By taking account only of those recaptures which occur within the marking area it is possible to estimate the fishing mortality coefficient in it and hence to determine c if the fishing intensity is known. Theoretically, this procedure is simple because it avoids having to deal with spatial variations in fishing intensity when using the recapture data, and the methods of analysis already discussed are directly applicable. The advantages of the method are largely practical ones, however. The marking area can be chosen reasonably near to port and where the commercial fishing intensity is high, thus obtaining as large a percentage recapture as possible and minimising statistical variation. It may also be possible to choose a marking area in which the variation of fishing intensity with time is large, so that methods making use of changes in intensity can be used (i.e. (14.19)). Finally, the method is particularly suitable for use in an area where several different fleets are operating but not all of which give reliable reports of the recaptures they obtain; in this case the marking area would be chosen as one in which the fishing effort is expended largely by the fleet that is most reliable for reporting recaptures. The main objection to the method arises if the rate of dispersion from the marking area is large, since it is necessary to treat this dispersion as part of the constant other-loss rate, X. Apart from the fact that changes in the rate of dispersion will cause X to fluctuate in an unknown way, recaptures of marked fish which have left the marking area cannot be used.

If the distribution of total effort over the whole exploited area is known, and if all sections of the fleet are equally reliable in reporting recaptures, a modification of this method can be used which largely obviates the objection arising from dispersion of marked fish from the marking area but which retains the practical advantages. This is to liberate marked fish in one or more convenient places where the fishing intensity and population density is high, to take account of all recaptures and to define the marking area as that from which, in a given period, recaptures are obtained. Thus as fish disperse after liberation, the area from which recaptures are obtained will increase in size, but this is of no consequence provided that the duration of each recapture period is not long. If the distribution of effort covers the greater part of the area occupied by the fish population so that no appreciable numbers of marked fish can disperse into areas in which there is no fishing, the total area from which recaptures are obtained during a given recapture period can be taken as defining the area occupied by the population of marked fish during that period. For the duration of each period the marked population can therefore be regarded as effectively a closed one, and by subdividing the recapture area into sub-areas small enough for the fishing effort to be regarded as distributed uniformly within each, the effective overall intensity in it for each period can be evaluated by means of (10.30) without taking specific account of the rate of dispersion. Thus we can modify (14.18) to become

$$n_r = \frac{c\tilde{f}_r N_0 e^{-\sum\limits_{p=0}^{r-1}(c\tilde{f}_p + X)\tau_p}}{c\tilde{f}_r + X}\left(1 - e^{-(c\tilde{f}_r + X)\tau_r}\right) \quad .. \quad .. \quad (14.23)$$

where $\tilde{f}_r$ is the effective overall intensity for the area from which recaptures are obtained during the rth period following liberation. Estimates of c and X can be obtained from (14.19) as before, and hence the effective overall fishing mortality coefficient for the whole exploited area can be computed from commercial statistics of catch and effort. With this method it is unlikely that values of $\bar{f}_r$ will be the same, if only because marked fish will disperse into areas of varying fishing intensities. If the values of $\bar{f}_r$ should happen to be effectively the same, it is of course possible to use the simpler methods of §14.1.1.1 to compute $\bar{F}$ and X, the former being the effective overall coefficient to be related to the value of f for the purpose of estimating c.

The above method can readily be adapted to enable recaptures from a number of separate liberations to be used. Thus for the rth period following liberation of the ith batch of marked fish we can compute an effective overall intensity ${}_i\bar{f}_r$, which is a weighted mean intensity with respect to the spatial variation in this quantity. For the rth periods following all liberations an intensity can also be computed which is a weighted mean of the values of ${}_i\bar{f}_r$ with respect to time, and which we denote by $\bar{f}_r'$. Denoting recaptures and fishing intensities referring to sub-areas by the prefixes α, β, ...ι..ω, the methods used to arrive at (10.30) for $\bar{f}_r$ and (14.21) for $\bar{f}_r'$ can be combined to compute $\bar{f}_r'$ as

$$\bar{f}_r' = \frac{\sum\limits_{i=a}^{z} \sum\limits_{\iota=\alpha}^{\omega} {}_{i,\iota}n_r}{\sum\limits_{i=a}^{z} \sum\limits_{\iota=\alpha}^{\omega} \frac{{}_{i,\iota}n_r}{{}_{i,\iota}f_r}} \quad .. \quad .. \quad .. \quad .. \quad (14.24)$$

Computing values of $\bar{f}_r'$ in this way enables recaptures from all liberations and all sub-areas to be used in (14.19) to estimate c and X. A possible source of variability of the estimates obtained with the above method arises if the majority of recaptures is from areas of high fishing intensity but a few are reported from areas where the intensity is very low. The normal sampling variation, or errors in giving the position of these few recaptures, would have a disproportionately large effect on the estimate of $\bar{f}_r'$ when appearing in the ratios of the denominator of (14.24), and in general it might be best to ignore any small numbers of recaptures from areas where the fishing intensity is relatively very low.

Finally, we should mention that a further method of analysing data of recaptures where the fishing intensity varies spatially is to take account specifically of the dispersion of marked fish. Since this method involves the estimation of the rate of dispersion it is best considered in connection with this problem in §14.1.2.4.

14.1.1.5 *Ricker's method of continuous marking*

Ricker (1948, pp. 62-63) has considered the case arising when marking is carried out continuously over a period of time at a constant absolute rate. This method is not readily applicable to a deep sea area, where weather conditions and distance from port may make marking spasmodic and uniformity difficult to achieve—difficulties which do not affect the methods previously discussed in which marked fish are liberated in batches. It has, however, one particular advantage, namely that it is not necessary to know how long each recaptured fish has been at liberty. The method can therefore be used when it is impossible to attach a numbered button or tag to the fish and they have to be marked by other methods (e.g. by mutilation).

The theory developed by Ricker concerns the case in which marking continues at a constant absolute rate throughout a fishing season and then stops. A correction factor is deduced to enable the total recaptures obtained during the first season while marking is in progress to be combined with recaptures from later years. There are, however, two possible ways in which the method can be extended to make it more adaptable to various practical conditions that may arise. One is to deduce methods for estimating F and X while marking is in progress, without requiring recaptures from later years; the other is to formulate it in a more general form that does not assume a constant rate of marking.

Both these requirements can be met by setting up the general equation defining the number of marked fish present at any time after marking has begun, which is

$$\frac{dN}{dt} = -(F + X)N + N^0(t)$$

where $N^0(t)$ denotes the rate of marking as a function of time. The solution for the number remaining after time t takes the form

$$N_t = e^{-(F+X)t}\int_0^t N^0(t)\, e^{(F+X)t}dt + Ce^{-(F+X)t} \quad .. \quad .. \quad (14.25)$$

where C is a constant of integration. The simplest case is when the marking rate is constant, and for purposes of illustration we consider only this case here, but it will be noted that $N^0(t)$ can be any reasonably simple function without leading to difficulties in integration. Thus it may be possible to make use of a steady trend in catches to mark many more fish than would be possible by adhering to a constant rate. It is also possible to approximate to continuous marking by liberating fish in batches, provided the number in each batch is small compared with the total number liberated, and the time interval between each batch is constant and short relative to the full period of marking.

From (14.25), with a constant rate of marking N^0, we have

$$N_t = \frac{N^0}{F+X} + Ce^{-(F+X)t}$$

Since $N_t = 0$ when $t = 0$, we have

$$C = -\frac{N^0}{F+X}$$

and

$$N_t = \frac{N^0}{F+X}\left(1 - e^{-(F+X)t}\right)$$

The rate of recapture is then

$$\frac{dn}{dt} = \frac{FN^0}{F+X}\left(1 - e^{-(F+X)t}\right)$$

and the number recaptured during the rth period of duration τ, from the beginning of liberation, becomes

$$n_r = \frac{FN^0}{F+X}\left\{\tau - \frac{(1 - e^{-(F+X)\tau})\, e^{-(F+X)(r-1)\tau}}{F+X}\right\} \quad .. \quad (14.26)$$

The ratio of any two successive returns is therefore

$$\frac{n_{r+1}}{n_r} = \frac{(F+X)\tau - (1 - e^{-(F+X)\tau})\, e^{-(F+X)r\tau}}{(F+X)\tau - (1 - e^{-(F+X)\tau})\, e^{-(F+X)(r-1)\tau}}$$

from which

$$F + X = \frac{n_{r+1} \cdot e^{(F+X)\tau} - n_r}{(n_{r+1} - n_r)\tau}\left(1 - e^{-(F+X)\tau}\right) e^{-(F+X)r\tau}$$

which provides a solution for $(F + X)$ by iteration. Putting this value of $(F + X)$ in (14.26) gives a solution for F.

The special case considered by Ricker is that arising if marking stops at the end of the first period of duration τ. Then the returns during the first period are given by

$$n_1 = \frac{FN^0}{F+X}\left(\tau - \frac{1 - e^{-(F+X)\tau}}{F+X}\right)$$

as before, but the returns during the second period are

$$n_2 = \frac{FN^0}{(F+X)^2}\left(1 - e^{-(F+X)\tau}\right)^2$$

so that

$$\frac{n_2}{n_1} = \frac{(1 - e^{-(F+X)\tau})^2}{(F+X)\tau - 1 + e^{-(F+X)\tau}}$$

and again we have a solution for $(F + X)$, and hence for F. The general term for recaptures in later periods, if marking stops at the end of the first period, is

$$n_r = \frac{FN^0}{(F+X)^2}\left(1 - e^{-(F+X)\tau}\right)^2 e^{-(F+X)(r-2)\tau} \quad .. \quad (14.27)$$

where $r \geqslant 2$, and the ratio of the successive terms becomes

$$\frac{n_{r+1}}{n_r} = e^{-(F+X)\tau}$$

so that a graphical solution for $(F + X)$ is possible from the later recaptures.

14.1.1.6 *Two sources of bias*

To conclude this discussion of fishing mortality we must mention two factors that may result in the estimate of F from marking data being different from the true value. The first of these is that the process of catching, marking and releasing a fish may result in its behaviour being abnormal to the extent that its liability to capture is different from that of unmarked fish. If this happens, the estimates of c, and hence F, though correct for the marked population, will not be applicable to unmarked fish. For example, if marking decreases the liability to capture, estimates of c obtained from marking experiments will be lower than that for the unmarked population. This factor is likely to be important only in those cases where the method of capture is particularly dependent on the behaviour of fish, as in a trap fishery, but if fish remain permanently affected we know of no direct method of correcting the estimates of c. More probably, however, fish will behave abnormally for a relatively short time after liberation, in which case unbiased estimates of c can be obtained by using (14.19) and allowing an appropriate period to elapse following liberation before recaptures are summed (see §14.1.2.1).

The second factor is the incomplete reporting by fishermen of the capture of marked fish. If we assume that a roughly constant proportion of recaptures is not reported, as is likely to be the case, the *ratios* of summed recaptures in successive periods would not be affected. Consequently, the methods for calculating F and X without using a knowledge of the initial number of marked fish liberated will give unbiased estimates of these parameters, since they make use only of ratios of recaptures (i.e. (14.19)). Methods involving N_0 however, while still giving unbiased estimates of the quantity $(F + X)$, as Ricker (1948) points out, will underestimate F and hence c. If they have to be used it may be possible to distinguish certain vessels or groups of vessels that do not report recaptures reliably. For example, in an internationally fished area the complete reporting of marks captured by vessels of countries other than that carrying out the marking experiment may be difficult to achieve. In such cases a possible procedure would be to discard all marks returned from such sources in the calculation of F and ignore the corresponding fishing effort in the estimation of f. In this way a more correct estimate of c might be obtained, the main criterion being that the fishing mortality caused by the non-reporting section of the fleet should be approximately constant, since it now becomes part of the other-loss rate X.

14.1.2 *Analysis of the 'other-loss' coefficient, X*

Hitherto, X has been taken as referring to the sum of all causes, other than fishing, of the reduction in number of an initial batch of marks. We have assumed that these causes act so that a constant fraction of the marks present is removed in any short period of given duration, that is to say,

$$_{X}\left(\frac{dN}{dt}\right) = -XN$$

We have been unable to develop rigorous methods for the direct estimation of X if this parameter is regarded as varying in an unknown way, though an indication of this might be obtained by analysing data of recaptures summarised in periods of several different durations (see §14.1.2.1).

Another approach is to distinguish the various components of the total other-loss coefficient and to attempt to estimate them independently. Several authors, e.g. Thompson and Herrington (1930), Graham (1938a) and Ricker (1948), have discussed possible causes of reduction of marks other than fishing; thus Ricker regards these factors as sources of 'error', and classifies them according to whether they affect estimates of total mortality, of fishing mortality alone, or of both. Two of these, namely the abnormal liability to capture of marked fish and the incomplete reporting of recaptures, have been discussed in §14.1.1.6 because they affect the estimation of F only; the remainder, comprising the other-loss coefficient X, are as follows:

(a) Mortality due to 'natural' causes, affecting marked and unmarked fish equally (e.g. predation, disease and possibly senility).

(b) Additional mortality of marked fish due to marking.

(c) Detachment of marks from living fish.

(d) Dispersion of fish from the marking area.

Sometimes the only object of a marking experiment is to estimate F and the true natural mortality (a), in which case the remaining causes can be treated as sources of error as Ricker suggests, and it is only necessary to eliminate their effect on the estimates of the main parameters. On the other hand, estimating the rate of dispersion, cause (d), may sometimes be of equal interest, and in the preliminary stages of a marking project it may be desirable to obtain estimates of the effects of causes (b) and (c) to decide on the best type of mark and method of marking. The question arises, therefore, of the extent to which the above components of X can be estimated separately.

Before attempting a further analysis we must distinguish two ways in which losses due to causes (b), (c) and (d) may be manifest. They may be restricted to a relatively short period immediately after liberation when they may be large and erratic (type (1)), or they may be present with roughly uniform magnitude throughout the marking experiment (type (2)). We discuss first the problems raised by type (1) losses.

14.1.2.1 *Correction for type* (1) *losses*

Ricker (1948, p. 65) has suggested a method of treating additional mortality due to marking and detachment of marks (causes (b) and (c)), in which "....fish of different degrees of apparent vigour, or fish tagged in different ways can be used". This method may be useful to give an indication of whether these causes are appreciable, though it almost certainly underestimates the true loss rates. Type (1) losses from causes (a), (b) and (c), however, can be dealt with by analytical methods if suitable data are available; in fact, the problem reduces to one of deriving equations giving solutions for F and X without requiring a knowledge of the initial number of marked fish liberated. This will, of course, be recognised as the same problem as that raised by the abnormal liability of marked fish to capture, and has already been mentioned briefly in §14.1.1.6.

Let us suppose that at a certain time t'_0 after liberation, type (1) losses are no longer operative, and that of the original number of marked fish liberated, N'_0 remain. We can then take it that 'other losses' are solely of type (2) and can be represented by the constant coefficient X. Bearing these definitions in mind, it is seen that (14.19) provides solutions for F and X without reference to N'_0—which in this case is unknown. In practice, the value of t'_0 would not be known directly, but a useful technique is to allow varying periods of time to elapse between the date of liberation and the beginning of the first recapture period, t'_0, disregarding all recaptures during these times, thus obtaining an indication of the variation of X with time. An estimate of t'_0 would then be given from the interval of time after liberation beyond which no further change in the value of X is found. If the values of F and X thus obtained are used in (14.15) and (14.16) it would be possible to compute an estimate of N'_0; since the number of fish recaptured prior to time t'_0 is known, a direct estimate of the total losses of type (1) can therefore be obtained by comparing the estimate of N'_0 with the actual number liberated. It is important to note that (14.19) can be used only if the fishing intensity changes over the period in question, and that the accuracy of the resulting estimates of F and X depends critically on the precision with which these changes can be assessed. In general, the importance of accurate data for fishing intensity if any detailed analysis of a marking experiment is to be attempted cannot be over-emphasized.

14.1.2.2 *Natural and marking mortalities*

If we take it that the effects of type (1) losses have been eliminated by a method such as that discussed above, the separate estimation of certain, but not all, of the steady residual losses, i.e. those represented by the constant coefficient X, is possible.

As far as we know, there is no direct way of obtaining the 'true' natural mortality (cause (a)) from marking experiments, that is, the value of the coefficient M for the whole population, although in favourable circumstances an approximate value might be obtained as the residue of X after all other components have been determined and subtracted.

Similarly, there would seem to be no direct method of estimating the additional mortality due to marking (cause (b)), but it may be possible to estimate its order of magnitude by trial experiments with different tags and by tank experiments, as suggested by Ricker. Fortunately, it is possible that in many instances fish surviving the rigours of the actual marking operation are then scarcely less healthy than the unmarked fish, in which case type (2) losses due to cause (b) may be negligible.

On the other hand, the effects of causes (c) and (d), namely detachment of marks from living fish and dispersion of fish from the marking area, are susceptible to direct analysis, and we now proceed to a discussion of methods for their estimation.

14.1.2.3 *Estimation of the rate of detachment of marks, L*

The method we describe for estimating directly the rate of detachment of marks from living fish makes use of a *double-marking* technique, each fish on liberation being tagged with two marks. The principle underlying this procedure is that some recaptures will still have both marks attached, but others will have one only; it is therefore possible to estimate the rate at which one mark is lost from two-mark fish, which under certain conditions will also be the rate at which marks are lost from one-mark fish.

The method by which the recapture data may be analysed depends on the particular hypothesis which is made concerning the similarities and differences between the behaviour of two-mark and one-mark fish, and in the following treatment we suppose that the total mortality rate of two-mark fish is the same as that of fish which originally had two marks but have lost one. It is not necessary, however, to assume that the other-loss rate X (which now excludes the decrease of a marked population resulting from the shedding of marks) is the same for these fish and normal one-mark fish, i.e. fish which have never had two marks. The methods developed below are applied in §14.1.3.2 to data obtained from a double-marking experiment on plaice.

The factors responsible for loss of marks from living fish are likely to be numerous and varied, probably depending to some extent on the particular environment of the fish and on any peculiarities in their behaviour, as well as on the type of mark and the method and position of its attachment to the fish. The effects of the majority of these factors cannot be distinguished or measured separately, but the work of Calhoun, Fry and Hughes (1951) on plastic deterioration and metal corrosion in Petersen disk tags has drawn attention to the serious shortcomings of some of the metals and plastics in common use for these tags. The estimates obtained by the double marking technique are, of course, of the total effect of all causes, but by carrying out an experiment at the same time and in the same areas as the main marking experiment, the estimates will be of the required loss-rate. We use the term 'event' to denote any happening which can *potentially* cause a mark to become detached from a fish, and suppose that the same number of events occur to both two-mark and one-mark fish per unit time. If it is assumed that the frequency of events is the same for fish which have become one-mark fish through the loss of a second mark as for normal one-mark fish, then estimates of the loss-rate of marks obtained by the double marking technique will apply to an ordinary marking experiment.

From the point of view of theoretical treatment we may group the causes responsible for shedding of marks into two types, as follows:

(i) Those whose effect on a mark does not depend on whether that mark is solitary or one of a pair, so that the marks behave *independently* (hypotheses (1) and (2)).

(ii) Those which are such that one mark can 'protect' the other (if present), so that marks behave *dependently* (hypothesis (3)).

Events resulting in loss of marks from the first type of cause may be either *local*—affecting one mark only even though a second mark may be present—or *general*, in which case both marks will be lost if there are two to lose. If there is only one mark present, the effect of a general event will be indistinguishable from that of a local event. Furthermore, two local events may occur simultaneously and cause both marks to be lost at the same time. Thus type (i) causes would include internal factors, such as the festering of a wound caused by attaching the mark; if necrosis is limited to the mark in question the event would be local, if it spreads to the second mark, although the latter would otherwise have remained attached, the event would be general. With the type of mark used for plaice, wear of the silver wire holding the ebonite buttons in position is a probable cause of loss of marks. External causes such as 'rubbing' would be included in this category, and might be either local or general according to whether the rubbed area included one mark only or both marks. For the case in which all the events leading to detachment of marks are local a solution for the loss-rate of marks can be obtained without difficulty, and we designate this by hypothesis (1). If some events are local and some are general we have been able to obtain a partial solution only; but this may be of value in giving limiting values (hypothesis (2)). If all events are general no one-mark fish will be recaptured and the method cannot be applied. In practice, this possibility could probably be minimised by not placing the marks too close together. Loss of marks from causes of type (ii) is likely to be less common, but an example is of one mark of a pair—probably the anterior—catching a piece of weed and thereby becoming detached, but preventing the second mark from damage. If only one mark is present this type of cause is, of course, indistinguishable from type (i).

Now it may happen that the rate of loss of an additional mark is not the same as that of the 'normal' mark, defining the latter as the mark occupying the normal position in an ordinary marking experiment. This may be because the additional mark is more or less firmly attached than the normal mark so that a given number of events would be less or more likely to result in the mark being lost, or because the frequency of events at the location occupied by the second mark differs from that at the normal location. Usually, however, it is possible to use marks with distinguishing features, so that when a one-mark fish is recaptured it is known whether this is the normal or additional mark. If this is so, it is possible (except in the case of hypothesis (2)) to take account of the fact that the loss-rate of the marks in the normal and abnormal position may be different; in fact, we shall find that the loss-rate from the normal position can be measured by attaching a second mark in another position and having a different loss-rate, and then dealing separately with the recaptures of one-mark fish which have lost either the normal or the additional mark. The methods required for this are more complex than if both marks have the same likelihood of becoming detached, and make greater demands on the data; in practice it would probably be best first to test whether there was any significant difference between the number of marks lost from each of the two positions,* and unless this was the case to proceed by the simpler methods in which the loss-rates are assumed equal. In the following treatment we give first the case of the loss rate being the same from both positions, designating these by hypotheses (1a), (2a) and (3a), and then show the modifications required when the loss-rate is different (hypotheses (1b) and (3b) only). It is not possible to distinguish from the recapture data alone which of the hypotheses (1), (2) and (3) gives the best representation of the actual process of loss of marks, but by obtaining estimates of the loss-rate according to each hypothesis it is possible to establish the probable limits within which the true value lies.

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*If the rate of loss of marks from the two positions is assumed to be the same, the relative number of one-mark recaptures from the two positions will vary according to the symmetrical binomial distribution, so that a test of significance is readily available.

A more detailed terminology than we have employed hitherto is required for the following analysis, and is as follows:—

(a) Hypotheses		(b) Hypotheses
L	Loss rate of marks in position A (the normal position)	${}_AL$
L	Loss rate of marks in position B	${}_BL$
${}_2N_0$	Number of double-marked fish liberated	${}_{A+B}N_0$
${}_1N$, ${}_1n$	Number of surviving fish and recaptures having the A-mark but not the B-mark	${}_{A-B}N$, ${}_{A-B}n$
${}_1N$, ${}_1n$	Number of surviving fish and recaptures having the B-mark but not the A-mark	${}_{B-A}N$, ${}_{B-A}n$

In addition, we define X^1 as the coefficient referring to the sum of all causes of reduction in the number of either two-mark or one-mark fish other than fishing and accidental detachment of marks, while F defines the fishing mortality coefficient which is assumed to be equal for both two-mark and one-mark fish. As before, the suffices ${}_1$, ${}_2$ are used to denote recaptures during the first and second recapture period respectively, each of duration τ years and, in addition, we use the suffix ${}_{1+2}$ to denote the sum of recaptures in both periods.

14.1.2.3.1 *Hypotheses* (1a) *and* (1b)

Since in hypothesis (1) we are supposing that detachment of marks is due to local events affecting each mark independently, the rate at which marks are lost from a given number of two-mark fish is twice as great as that from the same number of one-mark fish. Thus for hypothesis (1a) we have the rate of decrease in numbers of a population of two-mark fish given by

$$\frac{d\,{}_2N}{dt} = -(F + X' + 2L)\,{}_2N \qquad \ldots \quad \ldots \quad \ldots \quad (14.28)$$

so that the number of two-mark fish present after time t following liberation is

$${}_2N = {}_2N_0\, e^{-(F + X' + 2L)t} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.29)$$

As the two-mark fish lose a mark, a one-mark population is formed which loses marks at a rate per fish half that of the two-mark population. For the one-mark population we therefore have

$$\frac{d\,{}_1N}{dt} = -(F + X' + L)\,{}_1N + 2L\,{}_2N \qquad \ldots \quad \ldots \quad (14.30)$$

and substituting for ${}_2N$ from (14.29) gives

$$\frac{d\,{}_1N}{dt} = -(F + X' + L)\,{}_1N + 2L\,{}_2N_0\, e^{-(F + X' + 2L)t} \quad (14.31)$$

The number of one-mark fish present at any time t after the beginning of the experiment is therefore

$$ {}_1N = 2\,{}_2N_0\,e^{-(F+X'+L)t}(1-e^{-Lt}) \quad \ldots \quad \ldots \quad (14.32) $$

To obtain solutions for F, X' and L we may proceed as follows. The recaptures of one-mark fish throughout both periods of total duration 2τ is given from (14.32) as

$$ {}_1n_{1+2} = F\int_0^{2\tau} {}_1N\,dt = 2F\,{}_2N_0\left(\frac{1-e^{-(F+X'+L)2\tau}}{F+X'+L} - \frac{1-e^{-(F+X'+2L)2\tau}}{F+X'+2L}\right) \quad \ldots \quad (14.33) $$

while the number of two-mark fish recaptured during the first period is obtained from (14.29) as

$$ {}_2n_1 = F\,{}_2N_0\int_0^{\tau} e^{-(F+X'+2L)t}dt = \frac{F\,{}_2N_0}{F+X'+2L}\left(1-e^{-(F+X'+2L)\tau}\right) \quad \ldots \quad (14.34) $$

and during the second period as

$$ {}_2n_2 = \frac{F\,{}_2N_0\,e^{-(F+X'+2L)\tau}}{F+X'+2L}\left(1-e^{-(F+X'+2L)\tau}\right) \ldots \quad (14.35) $$

From (14.33), (14.34) and (14.35) we obtain the equation

$$ \frac{1-e^{-(F+X'+L)2\tau}}{(F+X'+L)2\tau} = \left(\frac{{}_1n_{1+2}}{2\,{}_2n_{1+2}}+1\right)\left\{\frac{1-\left(\frac{{}_2n_2}{{}_2n_1}\right)^2}{2\log\left(\frac{{}_2n_1}{{}_2n_2}\right)}\right\} \quad \ldots \quad \ldots \quad \ldots \quad (14.36) $$

which provides a solution for $(F + X' + L)$ by trial or from tables of the function $(1 - e^{-x})/x$ such as those compiled by Hardy (1918). Now from (14.34) and (14.35) we have

$$ F + X' + 2L = \frac{1}{\tau}\log\left(\frac{{}_2n_1}{{}_2n_2}\right) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.37) $$

so that we can obtain L by subtraction. With L thus determined, F and X' can be obtained in the usual way from (14.34) and (14.35).

Dealing now with hypothesis (1b), in which we suppose that the loss-rates from the two positions A and B are not the same, we can rewrite (14.28) in the form

$$ \frac{d\,{}_{A+B}N}{dt} = -(F+X'+{}_AL+{}_BL)\,{}_{A+B}N \quad \ldots \quad \ldots \quad (14.38) $$

For the one-mark population, on the other hand, it is now necessary to distinguish those fish which have lost the A-mark and those which have lost the B-mark. Thus for the former we have

$$ \frac{d\,{}_{B-A}N}{dt} = -(F+X'+{}_BL)\,{}_{B-A}N + {}_AL\,{}_{A+B}N \quad \ldots \quad (14.39) $$

and for the latter

$$ \frac{d\,{}_{A-B}N}{dt} = -(F+X'+{}_AL)\,{}_{A-B}N + {}_BL\,{}_{A+B}N \quad \ldots \quad (14.40) $$

Proceeding in a similar way as before, but using two-mark and A-mark recaptures only, we have an equation analogous to (14.36), viz.:

$$ \frac{1-e^{-(F+X'+{}_AL)2\tau}}{(F+X'+{}_AL)2\tau} = \left(\frac{{}_{A-B}n_{1+2}}{{}_{A+B}n_{1+2}}+1\right)\left\{\frac{1-\left(\frac{{}_{A+B}n_2}{{}_{A+B}n_1}\right)^2}{2\log\left(\frac{{}_{A+B}n_1}{{}_{A+B}n_2}\right)}\right\} \quad \ldots \quad \ldots \quad (14.41) $$

from which an estimate of the quantity $(F + X' + {}_AL)$ can be obtained by trial. In the same way, but dealing with two-mark and B-mark recaptures only, we have

$$\frac{1 - e^{-(F + X' + {}_BL)2\tau}}{(F + X' + {}_BL)2\tau} = \left(\frac{{}_{B-A}n_1 + 2}{{}_{A+B}n_1 + 2} + 1\right)\left\{\frac{1 - \left(\dfrac{{}_{A+B}n_2}{{}_{A+B}n_1}\right)^2}{2\log\left(\dfrac{{}_{A+B}n_1}{{}_{A+B}n_2}\right)}\right\} \quad \ldots \quad \ldots \quad (14.42)$$

which provides an estimate of $(F + X' + {}_BL)$. From (14.38) we have

$$F + X' + {}_AL + {}_BL = \frac{1}{\tau}\log\frac{{}_{A+B}n_1}{{}_{A+B}n_2} \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.43)$$

so that the estimates of $(F + X' + {}_AL)$ and $(F + X' + {}_BL)$ can be subtracted in turn from (14.43) to give estimates of ${}_BL$ and ${}_AL$ respectively. It will be noted that the solutions for L or ${}_AL$ and ${}_BL$ do not require a knowledge of the number of two-mark fish liberated, ${}_2N_0$, even though we are not making use of a known and varying fishing intensity, and this is also the case for the remaining two hypotheses discussed below. A further point is that for the (a) hypothesis we can use the sum of all one-mark recaptures during both periods, which is an advantage owing to the fact that they will always be much fewer in number than two-mark recaptures. For the (b) hypothesis, however, it is necessary to divide the one-mark recaptures into two groups according to whether the A- or B-mark has been lost.

14.1.2.3.2 *Hypothesis* (2a)

For hypothesis (1) we supposed that all the events which may lead to the detachment of a mark are local. We shall now postulate that of a given number of events only the proportion p is local, the remainder, q, being general and potentially capable of causing both marks to be lost simultaneously. We shall be able to deal only with the case in which the loss-rate at the two positions is the same.

When all events are local we found that a two-mark fish is twice as likely to lose one mark in a given time as is a one-mark fish. With general events, however, the likelihood of a two-mark fish losing both marks together is the same as that of a one-mark fish losing its single mark. Since we must suppose for hypothesis (2) that the total number of events—both local and general—per unit time is the same as in the case of hypothesis (1) when all were local events, we now find that the rate of decrease of the two-mark population is

$$\frac{d_2N}{dt} = \Big\{F + X' + L(1 + p)\Big\}_2N$$

so that

$${}_2N = {}_2N_0\, e^{-\{F + X' + L(1 + p)\}t}$$

The rate of loss of marks from the one-mark population is the same as before, but only p of the events happening to two-mark fish result in the loss of single marks, so that the rate of decrease of the one-mark population is now

$$\begin{aligned}\frac{d_1N}{dt} &= -(F + X' + L)\,{}_1N + 2pL\,{}_2N \\ &= -(F + X' + L)\,{}_1N + 2pL\,{}_2N_0\, e^{-\{F + X' + L(1 + p)\}t}\end{aligned}$$

The procedure from this point onwards is the same as in the case of hypothesis (1) and we need only state the final equations. Thus $(F + X' + L)$ may be obtained from an expression identical with (14.36), and from the two-mark recaptures we have

$$F + X' + L(1 + p) = \frac{1}{\tau}\log\left(\frac{{}_2n_1}{{}_2n_2}\right) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.44)$$

and

$$X' + L(1+p) = \frac{1}{\tau}\log\left(\frac{{}_2n_1}{{}_2n_2}\right)\left\{1 - \frac{{}_2n_1}{{}_2N_0\ 1 - \left(\frac{{}_2n_2}{{}_2n_1}\right)}\right\} \quad \ldots \quad (14.45)$$

Subtracting the estimate of $(F + X' + L)$ from (14.44) gives Lp, but it is not possible to obtain separate estimates of L and p. However, since the value of Lp obtained in this way is identical with that of L obtained from hypothesis (1a), the two hypotheses give the same value of L when $p = 1$, i.e. when all events are local. For any value of p less than unity, L of hypothesis (2a) will be greater than L of hypothesis (1a); so we reach the important conclusion that hypothesis (1a) tends to *underestimate* the true value of L according to how great a proportion of the total events is general. We can also obtain the maximum value of L by subtracting Lp from (14.45), leaving $X' + L$; this is, of course, the greatest value L can possibly have. In practice it would only be useful to know this if X' was small relative to L.

14.1.2.3.3 *Hypotheses* (3a) *and* (3b)

For hypothesis (3) we suppose that an event happening to a two-mark fish can remove only one of the two marks, the other being protected by the presence of the first. Thus the two-mark population is losing marks at the same rate per fish as the one-mark population, and for hypothesis (3a) we have

$$\frac{d_2N}{dt} = -(F + X' + L)\,{}_2N$$

giving

$${}_2N = {}_2N_0\, e^{-(F+X'+L)t} \quad \ldots \quad (14.46)$$

while for the one-mark population the equation is

$$\frac{d_1N}{dt} = -(F + X' + L)\,{}_1N + L\,{}_2N$$

Substituting for ${}_2N$ and solving the linear differential equation gives

$${}_1N = L\,{}_2N_0\, te^{-(F+X'+L)t} \quad \ldots \quad (14.47)$$

As before, we need expressions giving the recaptures of two-mark fish in the first and second recapture periods separately, and of one-mark fish in both periods together. Thus from (14.46) we have

$${}_2n_1 = \frac{F\,{}_2N_0}{F + X' + L}\left(1 - e^{-(F+X'+L)\tau}\right) \quad \ldots \quad (14.48)$$

and

$${}_2n_2 = \frac{F\,{}_2N_0\, e^{-(F+X'+L)\tau}}{F + X' + L}\left(1 - e^{-(F+X'+L)\tau}\right) \quad \ldots \quad (14.49)$$

while from (14.47) we have

$${}_1n_{1+2} = FL\,{}_2N_0\left\{\frac{1 - e^{-(F+X'+L)2\tau}}{(F + X' + L)^2} - \frac{2\tau e^{-(F+X'+L)2\tau}}{F + X' + L}\right\} \quad \ldots \quad (14.50)$$

Eliminating $F\,{}_2N_0$ and $F + X' + L$ from (14.48), (14.49) and (14.50) gives a direct solution for L, viz.:

$$L = \frac{{}_1n_{1+2}}{\tau\left\{\dfrac{{}_2n_{1+2}}{\log\left(\dfrac{{}_2n_1}{{}_2n_2}\right)} - \dfrac{2\,{}_2n_2{}^2}{{}_2n_1 - {}_2n_2}\right\}} \quad \ldots \quad (14.51)$$

so that F and X' can be obtained from (14.48) and (14.49) in the usual way.

When the loss-rate at position A is not the same as at position B, (hypothesis (3b)), the rate of decrease of the two-mark population becomes

$$\frac{d\,{}_{A+B}N}{dt} = -\left(F + X' + \frac{{}_AL + {}_BL}{2}\right){}_{A+B}N$$

and as with hypothesis (1b) we must distinguish between one-mark fish possessing the B-mark and those possessing the A-mark. Thus for the former we have

$$\frac{d\,{}_{B-A}N}{dt} = -\left(F + X' + {}_BL\right){}_{B-A}N + \frac{{}_AL}{2}\,{}_{A+B}N$$

while for the latter the equation is

$$\frac{d\,{}_{A-B}N}{dt} = -\left(F + X' + {}_AL\right){}_{A-B}N + \frac{{}_BL}{2}\,{}_{A+B}N$$

Obtaining expressions for ${}_{A+B}n_1$, ${}_{A+B}n_2$ and ${}_{B-A}n_{1+2}$ in the same way as for hypothesis (3a), we have

$$\frac{1 - e^{-(F + X' + {}_BL)2\tau}}{(F + X' + {}_BL)2\tau} = \left\{\frac{({}_AL - {}_BL)\,{}_{B-A}n_{1+2}}{{}_AL\,{}_{A+B}n_{1+2}} + 1\right\}\left\{\frac{1 - \left(\dfrac{{}_{A+B}n_2}{{}_{A+B}n_1}\right)^2}{2\log\left(\dfrac{{}_{A+B}n_1}{{}_{A+B}n_2}\right)}\right\} \quad .. \quad (14.52)$$

while the corresponding equation using the A-mark fish ${}_{A-B}n_{1+2}$ is

$$\frac{1 - e^{-(F + X' + {}_AL)2\tau}}{(F + X' + {}_AL)2\tau} = \left\{\frac{({}_BL - {}_AL)\,{}_{A-B}n_{1+2}}{{}_BL\,{}_{A+B}n_{1+2}} + 1\right\}\left\{\frac{1 - \left(\dfrac{{}_{A+B}n_2}{{}_{A+B}n_1}\right)^2}{2\log\left(\dfrac{{}_{A+B}n_1}{{}_{A+B}n_2}\right)}\right\} \quad .. \quad (14.53)$$

and these two equations together provide solutions for ${}_AL$ and ${}_BL$. Thus using (14.52) we may calculate values of ${}_AL$ for a series of trial values of ${}_BL$, and plot ${}_AL$ against ${}_BL$. If the reverse procedure is carried out using (14.53) we shall have two curves the intersection of which defines a pair of values of ${}_AL$ and ${}_BL$ satisfying both equations and which are therefore the solutions required. When this has been done, F and X' may be obtained from the two-mark recaptures in the usual way.

14.1.2.4 *Estimation of transport and dispersion coefficients*

In §14.1.2.1 we referred to dispersion as one of the factors responsible for the decrease in numbers of a population of marked fish in a restricted marking area, but often a knowledge of the rate of dispersion is of interest for its own sake, and may even be the main purpose of the marking experiment. The following methods are based on the theoretical treatment of §10.2 and for reasons given in §10.2.1 the emphasis is on the estimation of the transport coefficient T (§§14.1.2.4.1, 14.1.2.4.2). In §14.1.2.4.3 we give a brief outline of a method for estimating the true dispersion coefficient D.

14.1.2.4.1 *Transport from unequal sized areas*

The first method we discuss makes use of the concept, pointed out in §10.2.1 and following from an idea put forward by Jackson (1939) that a transport coefficient is by definition proportional to the perimeter/area ratio of the area to which it refers. In principle, it is to compare the rate of decrease of marked fish in two liberation areas similar in every respect except size.

Let us suppose that the total marking area B is a square with a perimeter/area ratio b, and that within it can be defined a smaller square A having a perimeter/area ratio a. Marked fish are released as uniformly and within as short a time as possible over the whole area B, note being kept of those liberated in area A. If the rate of dispersion is uniform over the whole area B, and provided the areas are not large, we can write (see §10.2.1)

$$_BT \simeq \frac{b}{a}\,{}_AT$$

We consider first the rate of decrease of marked fish in area B, that is, including those liberated in the inner area A. Immediately after being released, fish will begin to disperse across the outer boundary of area B with the result that the number remaining in it tends to decrease. However, as soon as there are fish outside area B there will be dispersion back into it, thus tending to decrease the effective loss from it. We define by $_{-B}N$ the number of marked fish outside area B at any time, and by $_{-B}T$ the transport coefficient defining their dispersion back into it across its outer boundary. Further, X' is defined as the sum of the 'other-loss' coefficients excluding transport, and in the first instance it is assumed that fishing is uniform over the whole of area B. In these circumstances, the rate of decrease of marked fish in area B can be written as

$$\frac{d\,{}_BN}{dt} = -\left(F + X' + \frac{b}{a}\,{}_AT\right){}_BN + {}_{-B}T\,{}_{-B}N \quad \ldots \quad \ldots \quad (14.54)$$

(compare (10.6)).

An analogous equation can be deduced for area A, referring in this case only to fish liberated in that area; thus

$$\frac{d\,{}_AN}{dt} = -\left(F + X' + {}_AT\right){}_AN + {}_{-A}T\,{}_{-A}N \quad \ldots \quad \ldots \quad (14.55)$$

where the product $_{-A}T\,{}_{-A}N$ refers to the dispersion back into area A of fish originally released in it but which had left it.

In order to obtain solutions of (14.54) and (14.55) it is necessary to make certain simplifying assumptions. If the whole marking area B is small relative to the area containing the population, $_{-A}T$ and $_{-B}T$ will be small compared with the transport coefficients $_AT$ and $_BT$ referring to outward dispersion. Further, since at time zero no fish will have dispersed from either area A or B, $_{-A}N$ and $_{-B}N$ will also be smaller than $_AN$ and $_BN$ provided t is not great. For a certain period after liberation the products $_{-A}T\,{}_{-A}N$ and $_{-B}T\,{}_{-B}N$ will therefore be small enough to ignore as a first approximation, in which case (14.54) and (14.55) become

$$\frac{d\,{}_BN}{dt} = -\left(F + X' + \frac{b}{a}\,{}_AT\right){}_BN$$

and

$$\frac{d\,{}_AN}{dt} = -\left(F + X' + {}_AT\right){}_AN$$

having solutions

$$_BN = {}_BN_0\,e^{-(F + X' + (b/a)\,{}_AT)t}$$

and

$$_AN = {}_AN_0\,e^{-(F + X' + {}_AT)t}$$

where $_BN_0$ is the number of marked fish liberated in area B and $_AN_0$ the number liberated in area A. The ratio of recaptures from area B during the first two periods, each of duration τ, is

$$\frac{{}_Bn_2}{{}_Bn_1} = e^{-(F + X' + (b/a)\,{}_AT)\tau}$$

while that from area A of fish liberated there is

$$\frac{{}_An_2}{{}_An_1} = e^{-(F + X' + {}_AT)\tau}$$

from which, by division,

$${}_AT = \frac{\log\left(\dfrac{{}_Bn_2}{{}_Bn_1} \cdot \dfrac{{}_An_1}{{}_An_2}\right)}{\tau\left(1 - \dfrac{b}{a}\right)} \quad \ldots \quad (14.56)$$

This treatment can readily be extended to deal with the case in which the effective overall fishing intensities differ in the two areas and during the two recapture periods. Thus the appropriate equations for ${}_Bn_1$ and ${}_Bn_2$ (see (14.18)) can give, by iteration, solutions for the quantity $X' + (b/a)\,{}_AT$; while those for ${}_An_1$ and ${}_An_2$ provide an estimate of $X' + {}_AT$. ${}_AT$ is then obtained by subtraction.

Despite its theoretical simplicity, use of this method in practice depends partly on whether recapture positions of marked fish are sufficiently accurate to permit sub-division of the smallest area within which dispersion can be taken as uniform. A further limitation is the need to disregard dispersion back into a marking area of fish that had previously left it after being liberated there. Both these objections can be overcome, or at least minimised, by taking specific account of fish that have dispersed from a marking area as well as of those remaining in it, which is the basis of the next method to be discussed.

14.1.2.4.2 *Transport between two adjacent areas*

Marking experiments involving direct measurement of interchange between adjacent areas can be planned in a variety of ways, but their analysis differs in detail only and follows the same basic methods discussed in §10.2.2. The example we consider here is a simple one and is based on the same layout as that used for the first method, except that area B is redefined as the annulus between the outer perimeter and that of the inner area A (i.e. it no longer includes area A). However, liberation is now restricted to area A and account is taken of fish that have dispersed from here into annulus B. This method therefore has an advantage over the first in that the area over which liberation must be accomplished as quickly as possible is smaller, and fuller use is made of recapture data: moreover, it is now possible to obtain estimates of the transport coefficient for each area separately.

Equations (10.9) and (10.10) give the yield from two adjacent areas between which there is continuous interchange of fish. In that case, however, it was assumed that the outer boundaries of both areas were closed, so that transport occurred between the areas only. In the present case there will also be dispersion of fish across the outer boundary of annulus B in both directions. Thus the basic differential equations (10.7) and (10.8) must be modified so that the rate of change of numbers in area A is

$$\frac{d\,{}_AN}{dt} = -\left({}_AF + X' + {}_AT\right){}_AN + p\,{}_BT\,{}_BN \quad \ldots \quad \ldots \quad (14.57)$$

and in annulus B by

$$\frac{d\,{}_BN}{dt} = -\left({}_BF + X' + {}_BT\right){}_BN + {}_AT\,{}_AN + {}_{-B}T\,{}_{-B}N \quad \ldots \quad (14.58)$$

The term $p_{B}T_{B}N$ of (14.57) defines the rate of movement of fish from annulus B across its inner boundary, that is, back to area A, p being the fraction of the coefficient ${}_{B}T$ referring to transport across this boundary; thus p is determined by the dimensions of annulus B, and is the ratio of the length of its inner boundary (the common boundary of areas A and B) to that of its total boundary length, both inner and outer. The term ${}_{-B}T_{-B}N$ of (14.58) has the same significance as in (14.54), and refers to dispersion back across the outer boundary of annulus B. Whereas in the previous method it was necessary to neglect dispersion back into both areas, it is now only necessary to do this in the case of the outer boundary of annulus B, since the number of fish in this annulus (and hence the term $p_{B}T_{B}N$ of (14.57) corresponding to ${}_{-A}T_{-A}N$ of (14.55)) can be assessed directly. Further, the error introduced by ignoring the term ${}_{-B}T_{-B}N$ of (14.58) is smaller than that of (14.54) since ${}_{-B}N$ now refers to fish, originally released in area A, that have first passed through annulus B and then returned across its outer boundary from a much larger area, and the number doing this is likely to be relatively small.

Integration of (14.57) and (14.58) can now be performed as described in §10.2.2. Putting

$$\left(\frac{{}_{A}F + {}_{B}F + {}_{A}T + {}_{B}T}{2} + X'\right) = \alpha$$

$$\sqrt{\left(\frac{{}_{A}F - {}_{B}F + {}_{A}T - {}_{B}T}{2}\right)^{2} + p\,{}_{A}T\,{}_{B}T} = \beta$$

and

$$\left(\frac{{}_{B}F - {}_{A}F + {}_{B}T - {}_{A}T}{2\beta}\right) = \gamma$$

and remembering that initially there are no marked fish present in annulus B, the recaptures in area A during the first and second periods of duration τ following liberation are given by

$${}_{A}n_{1} = \frac{{}_{A}F\,{}_{A}N_{0}}{\alpha^{2} - \beta^{2}}\left\{(\alpha + \beta\gamma)(1 - e^{-\alpha\tau}\cosh\beta\tau) - (\beta + \alpha\gamma)e^{-\alpha\tau}\sinh\beta\tau\right\} \quad .. \quad (14.59)$$

and

$${}_{A}n_{2} = \frac{{}_{A}F_{A}\,N_{0}e^{-\alpha\tau}}{\alpha^{2} - \beta^{2}}\left\{(\alpha + \beta\gamma)(\cosh\beta\tau - e^{-\alpha\tau}\cosh 2\beta\tau) + \right.$$

$$\left. + (\beta + \alpha\gamma)(\sinh\beta\tau - e^{-\alpha\tau}\sinh 2\beta\tau)\right\} \quad .. \quad .. \quad .. \quad (14.60)$$

In annulus B we have similarly

$${}_{B}n_{1} = \frac{{}_{A}T\,{}_{B}F\,{}_{A}N_{0}}{\alpha^{2} - \beta^{2}}\left\{1 - e^{-\alpha\tau}\left(\cosh\beta\tau + \frac{\alpha}{\beta}\sinh\beta\tau\right)\right\} \quad .. \quad .. \quad (14.61)$$

and

$${}_{B}n_{2} = \frac{{}_{A}T\,{}_{B}F\,{}_{A}N_{0}e^{-\alpha\tau}}{\alpha^{2} - \beta^{2}}\left\{\cosh\beta\tau - e^{-\alpha\tau}\cosh 2\beta\tau + \right.$$

$$\left. + \frac{\alpha}{\beta}\left(\sinh\beta\tau - e^{-\alpha\tau}\sinh 2\beta\tau\right)\right\} \quad .. \quad .. \quad .. \quad .. \quad (14.62)$$

These equations contain twelve parameters, viz.,

$${}_{A}n_{1}\,,\ {}_{A}n_{2}\,,\ {}_{B}n_{1}\,,\ {}_{B}n_{2}\,,\ {}_{A}N_{0}\,,\ {}_{A}F\,,\ {}_{B}F\,,\ {}_{A}T\,,\ {}_{B}T\,,\ X',\ p \text{ and } \tau$$

and if any eight of them are known, solutions can be found for the remaining four. For example, we shall usually know the initial number liberated, the four recaptures, the recapture period, and, in addition, the ratio ${}_{B}F/{}_{A}F$ from fishing effort statistics. In this case, therefore, only four unknowns, ${}_{A}F$, ${}_{A}T$, ${}_{B}T$ and X', remain.

Solution of these equations by trial and error is laborious, and it is convenient to obtain a first approximation to the unknowns by putting $p =$ zero, thus implying that there is no movement of marked fish from annulus B back into area A. Equations (14.57) and (14.58) can now be re-stated as

$$\frac{d\,{}_{A}N}{dt} = -({}_{A}F + X' + {}_{A}T){}_{A}N \quad .. \quad .. \quad .. \quad (14.63)$$

and

$$\frac{d\,{}_{B}N}{dt} = -({}_{B}F + X' + {}_{B}T){}_{B}N + {}_{A}T\,{}_{A}N \quad .. \quad .. \quad (14.64)$$

(14.63) can be integrated immediately to give the number remaining at any time in area A as

$${}_{A}N = {}_{A}N_0 e^{-({}_{A}F + X' + {}_{A}T)t} \quad .. \quad .. \quad .. \quad .. \quad (14.65)$$

and hence the recaptures in the first and second periods, each of duration τ, become

$${}_{A}n_1 = \frac{{}_{A}F\,{}_{A}N_0}{{}_{A}F + X' + {}_{A}T}\left(1 - e^{-({}_{A}F + X' + {}_{A}T)\tau}\right) .. \quad .. \quad (14.66)$$

$${}_{A}n_2 = \frac{{}_{A}F\,{}_{A}N_0 e^{-({}_{A}F + X' + {}_{A}T)\tau}}{{}_{A}F + X' + {}_{A}T}\left(1 - e^{-({}_{A}F + X' + {}_{A}T)\tau}\right) .. \quad (14.67)$$

If we now substitute for ${}_{A}N$ from (14.65) in (14.64) the latter becomes

$$\frac{d\,{}_{B}N}{dt} = -({}_{B}F + X' + {}_{B}T){}_{B}N + {}_{A}T\,{}_{A}N_0 e^{-({}_{A}F + X' + {}_{A}T)t} \quad .. \quad (14.68)$$

This is an ordinary linear differential equation of which the solution is

$${}_{B}N = \frac{{}_{A}T\,{}_{A}N_0}{{}_{A}F - {}_{B}F + {}_{A}T - {}_{B}T}\left(e^{-({}_{B}F + X' + {}_{B}T)t} - e^{-({}_{A}F + X' + {}_{A}T)t}\right) \quad .. \quad .. \quad (14.69)$$

so that the recaptures in annulus B are given by

$${}_{B}n_1 = \frac{{}_{B}F\,{}_{A}T\,{}_{A}N_0}{{}_{A}F - {}_{B}F + {}_{A}T - {}_{B}T}\left(\frac{1 - e^{-({}_{B}F + X' + {}_{B}T)\tau}}{{}_{B}F + X' + {}_{B}T} - \frac{1 - e^{-({}_{A}F + X' + {}_{A}T)\tau}}{{}_{A}F + X' + {}_{A}T}\right) \quad (14.70)$$

and

$${}_{B}n_2 = \frac{{}_{B}F\,{}_{A}T\,{}_{A}N_0}{{}_{A}F - {}_{B}F + {}_{A}T - {}_{B}T}\left\{\frac{e^{-({}_{B}F + X' + {}_{B}T)\tau}\left(1 - e^{-({}_{B}F + X' + {}_{B}T)\tau}\right)}{{}_{B}F + X' + {}_{B}T} - \right.$$

$$\left. - \frac{e^{-({}_{A}F + X' + {}_{A}T)\tau}\left(1 - e^{-({}_{A}F + X' + {}_{A}T)\tau}\right)}{{}_{A}F + X' + {}_{A}T}\right\} \quad .. \quad .. \quad (14.71)$$

Assuming that ${}_{A}n_1$, ${}_{A}n_2$, ${}_{B}n_1$, ${}_{B}n_2$, ${}_{A}N_0$ and τ are known quantities, and that we also know the ratio ${}_{B}F/{}_{A}F$ so that we may write

$${}_{B}F = \phi\,{}_{A}F \quad .. \quad .. \quad .. \quad .. \quad (14.72)$$

we may obtain solutions for ${}_AF$, X', ${}_AT$ and ${}_BT$ as follows. From (14.66) and (14.67) we have, in the usual way,

$$\left({}_AF + X' + {}_AT\right) = \frac{1}{\tau}\log\left(\frac{{}_An_1}{{}_An_2}\right) = \mathcal{J} \quad \ldots \quad \ldots \quad \ldots \quad (14.73)$$

and

$${}_AF = \frac{{}_An_1\,\mathcal{J}}{{}_AN_0\left(1 - \dfrac{{}_An_2}{{}_An_1}\right)} \quad \ldots \quad \ldots \quad \ldots \quad (14.74)$$

Dividing (14.71) by (14.70) and substituting for $({}_AF + X' + {}_AT)$ from (14.73) allows a solution for $({}_BF + X' + {}_BT)$ to be obtained readily by trial. Calling this latter quantity K, subtracting it from (14.73) and substituting for ${}_BF$ from (14.72) gives

$${}_AT - {}_BT = \mathcal{J} - K - {}_AF\,(1 - \phi)$$

so that

$${}_AT = \mathcal{J} - K - {}_AF\,(1 - \phi) + {}_BT \quad \ldots \quad \ldots \quad \ldots \quad (14.75)$$

Remembering also that

$$X' = K - \phi_A F - {}_BT$$

it will be seen that all quantities in (14.70) are now known except ${}_BT$, for which a solution can be obtained by trial. With these provisional estimates, and that of p obtained as already described, it is now possible to return to (14.59), (14.60), (14.61) and (14.62) to obtain more precise values for the parameters ${}_AF$, X', ${}_AT$ and ${}_BT$. An example of this procedure is given in §14.1.3.3.

14.1.2.4.3 *The point-release method for estimating dispersion coefficients*

So far we have discussed methods for estimating the transport coefficient T, which it will be remembered from §10.2.1 can be regarded as the finite difference equivalent of the instantaneous dispersion coefficient D. Practical considerations, such as the fact that the positions at which fish are recaptured and the distribution of fishing effort will be known only approximately, suggest that it will usually be easier to estimate transport coefficients than dispersion coefficients, but there is one requirement in the methods discussed above which may be difficult to achieve in practice, namely that marked fish should be distributed uniformly and effectively instantaneously over the area from which transport is to be measured. This particular difficulty can be overcome by what we call the *point-release* method, in which a batch of marked fish is released simultaneously in an area which is extremely small relative to that over which dispersion subsequently takes place, and it is then easier to estimate the dispersion coefficient. We have not used this particular method in the analysis of the plaice marking data given in §14.1.3.3 though some of it could be treated in this way, and it may be noted that Thompson and Herrington (1930) have studied dispersion in the Pacific halibut by arranging the data according to the distance from the point of release at which the fish were recaptured. In what follows we therefore give only an outline of the procedure required to estimate D by the point-release marking method.

In §10.2.1 the general differential equation

$$\frac{\partial C}{\partial t} = \frac{D}{4}\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right)$$

defined the dispersion coefficient in terms of the rate of change of density with respect to time and distance. A detailed discussion of this equation and its interpretation in the case of movement of fish is given in §15.1.2.1 where it is applied to an analysis of the off-shore migration of young plaice. Here it is sufficient to note that it is necessary to incorporate the mortality rate $(F + X')$, so that the equation becomes

$$\frac{\partial C}{\partial t} = \frac{D}{4}\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right) - (F + X')\,C$$

and has a solution*

$$C_{r,t} = \frac{N_0 e^{-(F+X')t - (r^2/Dt)}}{\pi D t} \quad \ldots \quad \ldots \quad \ldots \quad (14.76)$$

where $C_{r,t}$ is the density of marked fish at distance r from the point of release at time t, the initial number liberated at time zero being N_0.

The method used to estimate the rate of dispersion in experiments with mutant *Drosophila* (see Dobzhansky and Wright, 1943, 1947; Burla *et al*, 1950) was to compute the mean square distance from the point of release of recaptures at any given time after liberation, which is analogous to computing the standard deviation of a normal distribution. Although, in the present case, the magnitudes of the coefficients F and X' influence the density of marked fish at any given distance and time from release (see (14.76)), it can readily be shown that D can be estimated in the same way provided F and X' can be assumed constant in space and time. Thus the mean square distance of recaptures from the point of release at time t is given by the expression

$$\bar{r}^2 = \frac{\int_0^\infty r^2\, C_{r,t}\, 2\pi r\, dr}{\int_0^\infty C_{r,t}\, 2\pi r\, dr} \quad \ldots \quad \ldots \quad \ldots \quad (14.77)$$

and substituting for $C_{r,t}$ from (14.76) reduces (14.77) to

$$\bar{r}^2 = \frac{\int_0^\infty r^3 e^{-r^2/Dt}\, dr}{\int_0^\infty r e^{-r^2/Dt}\, dr} \doteq Dt \quad \ldots \quad \ldots \quad \ldots \quad (14.78)$$

so that by this means an estimate of D can be obtained which is independent of F and X', and also of the number liberated, N_0.

With a fishing intensity varying temporally or spatially, estimation of D by means of the point-release method presents considerable theoretical difficulties. A possible method of dealing with a non-uniformly distributed fishing effort would be to choose the release-point so that it lies within an area in which the distribution of fishing effort is reasonably uniform, and restrict analysis to recaptures within that area. In this case the mean square distance cannot be used to estimate D, but an estimate can be obtained from a knowledge of the mean density of marked fish at time t in a circular area of a given radius centred on the point of release.† Thus if we denote by $N_{r_1,t}$ the total number of marked fish in an area of radius r_1 at time t after release, we have from (14.76)

$$N_{r_1,t} = \frac{N_0 e^{-(F+X')t}}{\pi D t} \int_0^{r_1} 2\pi r_1\, e^{-r^2/Dt}\, dr$$

---

*This is analogous to equation (20) deduced by Skellam (1951a) expressing the combined effect of diffusion and geometric increase in a Malthusian population in a two-dimensional habitat.

†Daniels (1952) has suggested a method which need not involve an exact knowledge of the origin. The radius of the *covering circle* may be used as a convenient measure of dispersion, this being defined as the smallest circle containing every recovery point, or alternatively, every sampled value above a certain density. Daniels discusses the distributions of the centre and radius of this circle.

from which

$$N_{r_1,t} = N_0 e^{-(F+X')t}\left(1 - e^{-r_1^2/Dt}\right) \qquad \ldots \quad \ldots \quad (14.79)$$

The mean density of marked fish in the area at time t is therefore

$$\bar{C}_{r_1,t} = \frac{N_0 e^{-(F+X')t}}{\pi r_1^2}\left(1 - e^{-r_1^2/Dt}\right) \qquad \ldots \quad \ldots \quad (14.80)$$

Now, in practice, we shall not know the true mean density $\bar{C}r_1,t$, but by plotting the number of recaptures per unit effort from the area against time it would be possible to obtain an index of it, $\bar{C}'r_1,t$, where

$$\bar{C}_{r_1,t} = K\bar{C}'_{r_1,t} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (14.81)$$

and K is a constant. If, now, we estimate an index of the mean density of marked fish at a given time in two circular areas of radii r_1 and r_2, each centred on the point of release, we have from (14.80) and (14.81)

$$\frac{\bar{C}'_{r_1,t}}{\bar{C}'_{r_2,t}} = \frac{r_2^2\left(1 - e^{-r_1^2/Dt}\right)}{r_1^2\left(1 - e^{-r_2^2/Dt}\right)} \qquad \ldots \quad \ldots \quad \ldots \quad (14.82)$$

from which an estimate of D can be obtained by trial.

14.1.3. *Preliminary analysis of data from the English post-war plaice marking experiments*

Starting in May 1946, a series of marking cruises were made in the Southern North Sea by research vessels PLATESSA and SIR LANCELOT, working from Lowestoft. These cruises were of about five days' duration and several species of fish were marked, although plaice predominated. Numbered ebonite buttons were attached with silver wire which in the latter species was passed through the body near to the dorsal fin.

As has been mentioned previously, it would have been impossible to mark by density (see §14.1.1.4) over the whole of the Southern North Sea, and marking was therefore carried out on certain grounds conveniently near to Lowestoft which were known to have a high density of plaice and to be fished heavily, largely by British trawlers. Although marking was carried on intensively for more than two years, it is possible to give in this paper only an analysis of recaptures of plaice liberated during the first eight months, i.e. from May to December, 1946, but this will enable most of the theoretical methods developed previously to be demonstrated and gives provisional estimates of certain parameters.

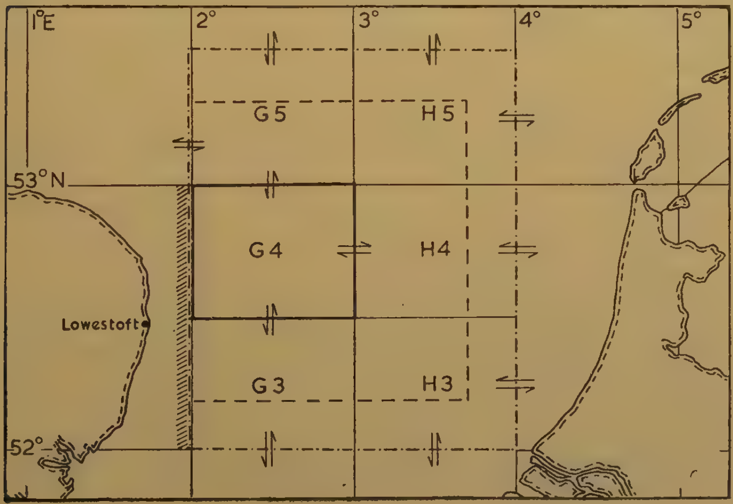

FIG. 14.1

PLAICE MARKING EXPERIMENTS

[Chart of main liberation areas of the English post-war experiments in the southern North Sea. Statistical rectangle boundaries are shown as – · – · –, the six concerned being G3, G4, G5; H3, H4, H5.]

We have stressed the need for estimating as accurately as possible the standardised fishing intensity that results in recapture of marked fish, and its changes with time. From the analysis of relative fishing power in part of the British North Sea trawler fleet (§12) it has been possible to compute the standardised fishing intensity per day due to British vessels in each of the six statistical rectangles G3, 4, 5; H3, 4, 5, for the year May 1946—April 1947 (see Fig. 14.1). This is the area to which by far the greater proportion of liberations and recaptures of marked fish refers, and we shall consequently deal only with liberations and recaptures by British vessels in those six rectangles.

14.1.3.1 *Estimation of fishing mortality and other-loss coefficients, F and X*

Table 14.2 summarises the recaptures of marked plaice in these six rectangles during the first two periods of 74 days (0.2 years) duration following liberation. These fish were liberated during twenty-three marking cruises of the PLATESSA made during 1946, and the data from all these cruises and rectangles were combined by the method suggested in §14.1.1.4 (equation (14.24)), to give estimates of the effective overall fishing intensities in the marking area, $\tilde{f}_1'$ and $\tilde{f}_2'$, given in Table 14.2, these being in the units 'S/T ton-hours/square mile/year $\times 10^{-3}$.'

With two recapture periods we need both (14.19) and (14.20) to obtain separate estimates of c and X. Iteration proceeds by first putting the second logarithmic term of (14.19) to zero, thus obtaining the first estimate of $(c\tilde{f}_1' + X)$, and then separating the two coefficients by means of (14.20). These estimates are then used to compute the whole of the left hand side of (14.19), giving a second estimate of $(c\tilde{f}_1' + X)$, and hence of c and X from (14.20) as before. The steps in performing this iteration are set out in the work-sheet shown in Table 14.3. It will be seen that successive estimates of c and X form a rapidly converging series with the second approximations correct to three decimal places, the figures being

$$c = 0.21$$

$$X = 7.08$$

This value of c gives the effective overall fishing mortality coefficients in the marking area in the two periods as

$$\tilde{F}_1' = 1.25$$

$$\tilde{F}_2' = 1.14$$

We may obtain another, and to some extent independent, estimate of c by restricting analysis to those fish both liberated and recaptured in the most highly fished of the six rectangles, i.e. G4. These data are summarised in Table 14.4, and by use of the same iterative method as before we obtain the values

$$c = 0.18$$

$$X = 9.71$$

$$F_1' = 1.79$$

$$F_2' = 1.96$$

It will be seen that although the fishing intensity and fishing mortality coefficients in G4 are considerably greater than in the six rectangles as a whole, the estimates of c from each source are in reasonably good agreement. Further, X for G4 is also higher than for the six rectangles combined, which suggests that there may be a fairly high rate of dispersion of fish from the marking area. This point is discussed further in §14.1.3.3.

By grouping recaptures in 37 day periods ($\tau = 0.1$ years) we can deal with three successive recapture numbers n_1, n_2, and n_3, and the data from which Table 14.4 was compiled are rearranged in this way in Table 14.5. By similar methods we obtain from n_1 and n_2

$$c = 0.26$$

$$X = 12.90$$

and from n_2 and n_3

$$c = 0.24$$

$$X = 9.90$$

giving an average value of

$$c = 0.25$$

The difference between these two values of X suggests that type (1) losses are not inconsiderable, but we have not been able to obtain reliable estimates of c and X by means of (14.19) from these data. This is because after allowing a sufficient period of time to elapse following liberation, the number of recaptures was not large enough to group into as many recapture periods as would be desirable, and also that the variation in fishing intensity was small, thus throwing too great a strain on the accuracy of the recapture data and of the commercial statistics of fishing time. Until the results of the whole post-war marking experiments have been analysed we shall therefore take the above values as our best estimates of c. Moreover, since the existence of type (1) losses will tend to make these values too low, we shall use the highest value found, i.e.

$$c = 0.25$$

in further calculations.

14.1.3.2 *Estimation of the rate of detachment of marks*

We now proceed to a further analysis of certain components of the other-loss rate X, the first of these being the *rate of detachment of marks from living fish*, L. During a cruise of the research vessel SIR LANCELOT in May 1947 in the Southern North Sea, 516 double-marked plaice were liberated at Smith's Knoll (rectangle G4). It was not possible for the following analysis to assess changes in fishing intensity in the area from which recaptures were obtained so it will be necessary to suppose that F remained constant throughout. To make some allowance for possible changes in fishing intensity however, we have summed the recaptures in three ways, with $\tau = 1.0$, 0.5 and 0.25 years respectively. Recaptures of two-mark fish during each recapture period are given in columns A and B of Table 14.6, while the one-mark recaptures during both periods are given in column C.

It will be remembered that in §14.1.2.3 we put forward three hypotheses to account for the possible ways in which marks might become detached, and in the case of hypotheses (1) and (3) the treatment differed according to whether the loss-rate from the normal and additional positions was the same or different. In the present experiment the additional mark was attached behind the normal mark and about one to two inches from it, so that we would not expect to find that the loss-rate differed. This was borne out by the fact that of the 20 one-mark fish recaptured during the two years following liberation exactly half had lost the normal mark and half the additional mark. In the following analysis we therefore need consider the (a) hypotheses only.

In Table 14.7 are summarised the estimates of F, X' and L using (14.34), (14.35) and (14.36) for hypothesis (1a) and (14.48), (14.49) and (14.50) for hypothesis (3a). Only one series of values of F is given, since all hypotheses give the same estimate of this parameter. It will be seen that the estimates of L increase as τ increases, as do those of F and X', and the indications are that all three parameters were varying during the course of the experiment. It will be seen, however, that all the estimates of L obtained by means of hypothesis (1a) are lower than those of (3a), and since we showed in §14.1.2.3.2 that the former must be regarded as the minimum values of L in so far as there is any tendency for events to remove both marks together, we must put the lowest value of L at about 0.2. Since X' is much greater than any of the values of L we cannot obtain any useful estimate of the maximum value of L by putting $X' = 0$, but it is unlikely that L is greater than the largest value obtained from hypothesis (3a), i.e. 0.4.

From the results of this double-marking experiment it would seem that the loss-rate of marks used in the marking experiments discussed previously is probably between 0.2 and 0.4. This is not a large proportion of the total other-loss rate which we have found, but in itself is not negligible. For example, it implies that a given number of marked fish would be reduced to about 75% of their initial number during the course of a year through detachment of marks, even if no mortality of any kind occurred. In this connection it is relevant to note that silver wire was used in the above experiment to attach the discs, and that this metal is regarded as unsatisfactory by Calhoun, Fry and Hughes (1951) owing to the ease with which it can be work-hardened. On the other hand, the discs used in English plaice-marking experiments are made of ebonite—a material not examined by these authors—and there is no record from many thousands of recaptures over a number of years of one showing any signs of deterioration or damage.

14.1.3.3 *Estimation of transport coefficients*

Certain differences in the various values of X obtained in §14.1.3.1 have already been noted and tentatively attributed to the existence of a not inconsiderable dispersion rate. The post-war plaice marking experiments were not designed to provide estimates of transport coefficients, and they do not satisfy in detail the requirements suggested in §14.1.2.4, but an idea of the order of magnitude of T can nevertheless be obtained from the data. This is of value, despite its approximate nature, in view of the virtual absence of quantitative information on dispersion in any fish population, and also for comparison with the estimate of the dispersion coefficient D given in §15.1.2.1, obtained from data of an entirely different kind. For this purpose we shall refer to the data already quoted and to Fig. 14.1, which is a map of the area in which marking was carried out.

If we define rectangle G4 as area A, and area B as the total of the six rectangles, then we may obtain a preliminary estimate of ${}_AT$ by using the first method (§14.1.2.4.1) although the conditions required for this method, i.e. random distribution of marks over area B, were not strictly satisfied. From the data of Table 14.2, and remembering that X' now refers to other-losses excluding transport, we have

$$F + X' + {}_BT = 8.33 \text{ (Table 14.3, column } N_2\text{)}$$

and

$$F = 1.25 \text{ (,, ,, ,, } P_2\text{)}$$

Hence

$$X' + {}_BT = 7.08 \quad \ldots \ldots \ldots \ldots \ldots \quad (14.83)$$

Similarly, for area A, we have from the data of Table 14.4,

$$F + X' + {}_AT = 11.50$$

and

$$F = 1.80$$

so that

$$X' + {}_AT = 9.70 \quad \ldots \ldots \ldots \ldots \quad (14.84)$$

We have now to determine the relationship between ${}_AT$ and ${}_BT$. We may first note that practically no deep sea trawling takes place between the shore and the western boundaries of rectangles G3 and G4, and in fact the latter probably coincide roughly with the natural limits of distribution of the main adult plaice population. Consequently we shall take it that dispersion from area A (G4) occurs only across its northern, eastern and southern boundaries, and dispersion from area B occurs over its whole perimeter except the western boundaries of G3 and G4. Consequently, the open-boundary/area ratio for area A is

$$a = \frac{3}{1}$$

and that for area B is

$$b = \frac{8}{6}$$

Thus we have, to a first approximation,

$${}_bT = \frac{b}{a}\,{}_AT = 0.444$$

and hence, from (14.83) and (14.84) we have

$$0.555\ {}_AT = 9.70 - 7.08$$

so that

$${}_AT = 4.7$$

A better estimate of ${}_AT$ can be obtained by the second method described in §14.1.2.4.2, and for this purpose we retain the same definitions for area A, defining 'annulus B' as the five rectangles, G3, G5, H3, H4, H5, and restricting analysis to fish liberated in G4 only. The recaptures during the first and second periods, from both this area and the annulus B, are given in Table 14.8. In addition, we found from commercial statistics that the ratio of the effective overall fishing intensities in the respective areas was $\phi = 0.3$, this and the intensities themselves being nearly enough constant over the two periods.

We first analyse these data by means of (14.66), (14.67), (14.70) and (14.71), which it will be remembered are the simpler expressions obtained by putting the factor p equal to zero and hence neglecting dispersion back into area A of fish that had previously left it. These give the results

$${}_AF = 1.76$$

$${}_AT = 10.97$$

$${}_BT = 20.73$$

$$\text{and } X' = -1.62$$

The negative value of X' is clearly absurd, and we have reason to believe that our stated value of ϕ is something of an underestimate, since fish in annulus B are certainly concentrated near its inner boundary and the fishing intensity is higher here than in the annulus as a whole. Statistics of fishing intensity are insufficiently accurate to give precise information on this point, but the distribution of known fishing grounds would indicate that ϕ may contain an error rather greater than 50%, the true value probably being more nearly 0.5. If we use this value we obtain the following estimates

$${}_AF = 1.76$$

$${}_AT = 7.84$$

$${}_BT = 17.21$$

$$\text{and } X' = 1.51$$

Before these can be used as first approximations in (14.73-76), we must first decide the best value of p to use. From dimensional considerations alone this is given by the ratio

$$\frac{3}{11} = 0.27$$

but since, if anything, the fish are concentrated within an effective annulus somewhat smaller than area B, we shall use the value

$$p = 0.3$$

Approximate solutions of these equations were then obtained by making about twenty-five trial computations. With this number of trials it was not possible to find a set of parameter values that would reproduce the observed recaptures to within a whole number, but the set

$$\left.\begin{aligned} {}_AF &= 1.9\\ {}_BF &= 1.05\\ {}_AT &= 7.0\\ {}_BT &= 14.0\\ X' &= 4.5\\ p &= 0.3\\ N_0 &= 6717\\ \tau &= 0.2 \end{aligned}\right\}\text{ gave }\left\{\begin{aligned} {}_An_1 &= 951\\ {}_An_2 &= 106\\ {}_Bn_1 &= 164\\ {}_Bn_2 &= 42 \end{aligned}\right.$$

From the previous discussion it will be appreciated that there are only four independent unknown quantities among the eight parameters listed here, i.e. ${}_AF$, ${}_AT$, ${}_BT$ and X'. The above estimates of these are not strictly the most probable ones, but the agreement between the predicted and observed recaptures is so close that they can reasonably be taken as good enough for our purposes. Moreover, there was no indication during the trial computations that any widely different set of values would give the same, or nearly the same, recaptures.

It will be noticed that the estimate of ${}_AT$ obtained by the first method is of the same order as that given above and that the difference between the results of the two methods is in the expected direction* and not greater than would be expected from the fact that the marked fish were concentrated away from the outer perimeter of annulus B, which is contrary to the requirements of the first method. The values of p and ϕ that we have used in the above example are consistent with the suggestion that the effective outer perimeter of the annulus is about 10 miles within the actual boundaries of the rectangles concerned, as shown by the broken lines (— — · —) of Fig. 14.1.

Since the perimeter/area ratios of area A and annulus B are about the same if the outer perimeter of B is redefined as suggested above, the difference between the values of ${}_AT$ and T obtained by the second method can be taken as indicating a real difference between the rate of movement of fish in the two areas, it being remembered that we have not had to postulate that the difference between ${}_AT$ and ${}_BT$ is solely determined by the dimensions of the areas in question, as was necessary in the first method. It is possible that some of the difference between ${}_AT$ and ${}_BT$ is due to abnormal behaviour of marked fish; more specifically, certain individuals may react to marking by increased activity, in which case it would be these fish that would be most likely to move first into annulus B and thus tend to give a higher value for ${}_BT$ than for ${}_AT$, though provided the *mean* speed of movement of a group of marked fish is not abnormal ${}_AT$ should not be affected. We must therefore regard our estimate of ${}_AT$ as being more reliable than that of ${}_BT$, but that most of the difference between the two coefficients reflects a true difference in rate of dispersion in the two areas (i.e. of unmarked as well as marked fish) is confirmed by examining the relative magnitudes of commercial catches and fishing intensities. In Table 14.9 are given the fishing intensity, catch and density of plaice for G4 and the mean values for the rectangles comprising annulus B, these figures being averages of the four years 1947-50. It is found that both the intensity *and* catch in G4 are about four times as great as in the other rectangles; this must mean that the tendency for fish to aggregate in G4 is much greater than it is in the other rectangles, and hence confirms that the transport coefficient ${}_AT$ must be considerably smaller than ${}_BT$. It is interesting and important to note how the fleet distributes itself in such a way as to maintain an almost equal density in both areas and thus satisfies part of the requirements for generating the maximum possible fishing mortality which we put forward in §10.3, namely that the distribution of fishing effort should be such as to maintain the densities roughly equal in all those areas in which the fish show the greatest tendency to aggregate.

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*Since the first method does not take into account the movement of fish back into the marking area A, it would be expected to give an underestimate of the true value of ${}_AT$.

The rate of interchange of fish between adjacent rectangles implied by the values of the transport coefficients determined above is considerable. For G4, during the season when the marking experiment was carried out, the above value of ${}_AT$ implies that about 80% of the fish present at any moment would cross its boundary at least once during the following three months, while for the remaining rectangles the figure would be above 90%. It may be that these estimates of transport are exaggerated by inaccurate reporting of recapture positions, but their order of magnitude nevertheless agrees with an estimate of the instantaneous dispersion coefficient D obtained in §15.1.2.1 from a different kind of data in which this source of bias is absent. We have not been able, for this paper, to analyse the plaice marking data by the point-release method outlined in §14.1.2.4.3, although in certain later cruises a large number of fish (up to 5,000) were marked and released in a single small area and the data from these should therefore be suitable for treatment in that way.

Although transport can apparently account for the greater part of the other-loss coefficient X—perhaps more than two-thirds—the residue seems still too large to be ascribed to 'true' natural mortality, even allowing for the rate of detachment of marks estimated in §14.1.3.2. Other methods will be used to estimate M, and these are presented in §14.3.2.3.

14.2 Variation of the Fishing Mortality Coefficient with Size of Fish—Mesh Selection

We have previously mentioned, in §14.1.1.3, the use of marking experiments to investigate changes in F with age of fish. A particular aspect of this problem concerns changes in F due to the selective action of gear, and can be studied by means of comparative gear experiments. We do not propose to undertake a detailed discussion of the problem of gear selectivity, and shall deal primarily with the methods of deriving the selection ogives of the cod-ends of otter trawls used by British vessels, since it has been generally accepted that the greater part of the selective action of these trawls occurs in the cod-end, particularly for flat-fish (Todd, 1911).

Davis (1934) and Jensen (1949), in particular, have discussed the various experimental techniques that have been used to study the selective action of cod-ends, viz.:

(i) Experiments with covered cod-ends.

(ii) Experiments with trouser-trawls.

(iii) Alternating or parallel hauls with small and large meshed cod-ends.

Davis was not satisfied that a covered cod-end fished normally and, indeed, showed experimentally that fitting a cover caused a cod-end to retain relatively more smaller fish. He regarded the parallel haul method* as the best for testing a specified mesh under conditions closest to those of commercial use, but was in favour of the trouser-trawl method for experimental purposes and pointed out that bias between the two legs of the trouser cod-end could be eliminated by changing them over between hauls. On the other hand, certain factors such as the tension of meshes and the flow characteristics in a trouser cod-end can scarcely be identical with those in a single cod-end of the same mesh size, so there is the possibility that neither leg has truly normal selectivity. The alternate or parallel haul method would seem *a priori* likely to involve the least systematic error but has the disadvantage that between-haul sampling variation may sometimes be large—whether hauls are made contemporaneously by two vessels or successively by one. It has been found, however, in experiments on plaice carried out by the Lowestoft Laboratory since the war, that this sampling variation was not enough to prevent alternate hauls by a research vessel from giving satisfactory results, while the very large number of parallel hauls in the commercial experiment on haddock conducted by Davis effectively minimises sampling variation. In the following we therefore derive selection ogives and selection factors for plaice and haddock from these two sources of data.

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*Davis treated alternate hauls with different cod-ends by a single vessel and parallel hauls by a pair of vessels using different cod-ends exchanged between each haul as separate methods. The difference between them, however, concerns mainly, if not entirely, the degree of sampling variation which, according to the circumstances, may be in favour of either method.

14.2.1 *Plaice—the alternating haul method with large and small meshes*

Let us suppose that we wish to obtain the selection ogive for a cod-end (A) of a given mesh size. The simplest procedure is to make a series of pairs of hauls of equal duration and towing speeds, and on the same grounds, with the trawl fitted alternately with cod-end (A) and with a cod-end (B) whose mesh is considerably smaller. If the mesh size of cod-end (B) is such that its selection range is below that of cod-end (A), its catch in numbers of fish of each length per unit fishing time is a true index of the length distribution of the population within the selection range of cod-end (A). If these conditions are satisfied, then the ratios of the catch in numbers at each length per unit fishing time of cod-end (A) to that of (B) give a first estimate of the selection ogive for the larger cod-end.

We may cite from experiments of this kind on plaice carried out recently from Lowestoft. It was found that between eight and twelve pairs of hauls were usually sufficient to give reasonably consistent results, and grounds were chosen that were known to hold quantities of plaice of lengths within the anticipated selection range of each particular cod-end to be tested. The duration of haul (three hours) was typical of that used by commercial trawlers. Cod-end meshes were measured frequently during the experiments by means of a flat triangular brass gauge inserted as far as possible into the mesh without forcibly stretching it. The mesh sizes given are therefore the inner lengths of the long diagonal of the diamond of the extended mesh. The cod-ends in all experiments were of untarred double white sisal, and the sizes of the four pairs of cod-ends investigated (means of a number of measurements during use) were as follows:

Small mesh (mm.)	Large mesh (mm.)
43.2	72.2
44.1	111.9
43.2	113.0
44.5	140.6

Table 14.10 (columns A, B, C and D) gives the ratios of the total catches obtained for equal fishing times by each of the four pairs of cod-ends. The approximate selection range in each case can be seen by inspection as the range of length over which the ratios increase rapidly from zero, but for reasons mentioned below we also need to find whether the data show a trend at greater lengths. The values plotted in Figs. 14.2 are therefore the actual data of Table 14.10 for the selection ranges, but smoothed by moving averages of five at greater lengths to minimise the fluctuations due to small numbers and to show whether a trend exists. None of these graphs is of the shape we might expect if differences were due entirely to selectivity, namely a symmetrical ogive with a lower asymptote of zero and an upper of unity. That of Fig. 14.2.2 for the 111.9 mm. mesh is perhaps the nearest approach

to this, while Fig. 14.2.4 for the 140.6 mm. mesh seems to tend to an upper asymptote appreciably greater than unity, in fact about 1.2. The 72.2 and 113.0 mm. meshes, Figs. 14.2.1 and 14.2.3, present an additional complication: not only do the ratios reach values greater than unity, but after reaching their maximum values they then decrease roughly linearly, this trend being noticeable despite the large variation due to sampling error in the small numbers of fish caught at the greater lengths. These characteristics have a bearing on the problem of determining the selective properties of the cod-ends and must be considered further.

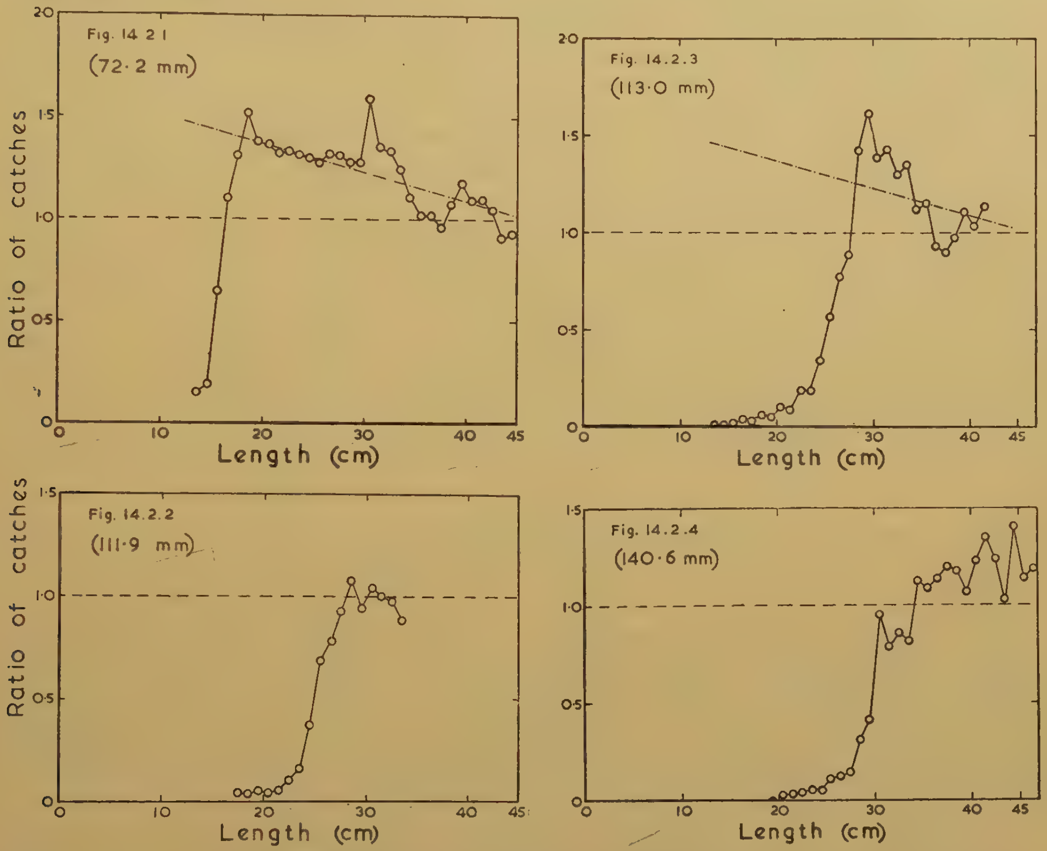

FIG. 14.2 PLAICE MESH SELECTION

[Ratios of numbers caught per unit fishing time by large- to small-meshed cod-ends plotted against length of fish; from Table 14.10. In three of the four experiments catches by the larger mesh exceeded those by the smaller beyond a certain length, and adjustments are required to obtain the true-selection ogives (see Fig. 14.3).]

The observation that the ratios reach a level greater than unity may be due to one or both of the following causes. Either the greater catches of the larger-meshed cod-end are due to sampling variation, i.e. this cod-end happened by chance to fish a rather denser population, or else they are due to a real increase in efficiency of the trawl fitted with the larger meshed cod-end. We have not investigated this point in detail, but although the data from any one experiment are unlikely to be extensive enough to provide an adequate statistical test, the fact that the same phenomenon has been found by other authors (e.g. Davis, 1934), and that many of the experiments conducted from Lowestoft in recent years agree in this respect, suggests that a real difference in efficiency does exist. For the present purposes, however, it is quite immaterial which of the two causes is operative. By summing the catches at each length of each cod-end and then taking ratios we are, in effect, combining the data to give one large experiment, the data from the individual hauls being weighted in proportion to the number of fish caught. As a weighting method this may not be the best, but it is not likely to cause much error unless, for example, the actual selective properties of the gear vary according to the magnitude of the catch owing to congestion of the meshes, which is unlikely in the experiments under discussion.

It is sufficient, therefore, to note that more fish of lengths beyond the selection range did, in fact, reach the larger-meshed of the two cod-ends in all but one case, and it is reasonable to suppose that the same is true for fish within the selection range though, of course, this cannot be seen from the data. If, however, the ratios of the catches at each length above the selection range vary in a regular way, we can obtain an adequate adjustment of the data within that range by extrapolation, a procedure also followed by Davis (ibid) when dealing with mesh selection data. When doing this it is desirable that the fish in question should not segregate into shoals within each of which the size range is small, and that the selection range should not be too large a part of the total range of length covered by the data; both these criteria are reasonably satisfied in the plaice data we are discussing, in which none of the adjustments we shall make alter the location of the ogives by more than a centimetre*.

Data from columns A, B, C and D of Table 14.10 adjusted according to the above procedure are shown in columns E - H of the same table. It seemed unnecessary to adjust the data of column B for the 111.9 mm. mesh, but for comparative purposes the data are repeated in column F. For the 140.6 mm. cod-end, however, we have divided the ratios of column D by the factor 1.2, the result being given in column H. The data for the 72.2 and 113.0 mm. cod-ends have been adjusted by extrapolating linear regressions. Taking the origin as corresponding with a fish length of zero, the regression coefficients of the equation

$$y = a_0 + a_1x$$

were taken as

$$a_0 = 1.65$$

and

$$a_1 = -0.014$$

for both meshes. The ratios in columns A and C were therefore divided by the appropriate value of y at each length, the adjusted ogives being tabulated in columns E and G. It is of interest to note that the two cod-ends which showed a regression were those used by the research vessel SIR LANCELOT, the other two being used by the PLATESSA. Further analysis of the behaviour of the gear of these two vessels may throw light on this matter†, but it seems that a proper treatment of the relationship between mesh size and gear efficiency requires further experimental data than is yet available and we cannot attempt it here.

The four adjusted ogives are plotted in Figs. 14.3, the points above the selection range being derived from the smoothed values of Table 14.10. The points within the selection ranges are joined by smooth freehand curves, which give the 50% selection lengths with some accuracy since the data allow very little latitude for drawing the ogive in this region, and the values for each mesh are given in column B of Table 14.11. To these we may add further estimates of the 50% points of seven other meshes which have been studied experimentally from Lowestoft. These latter experiments were made before the small-meshed cod-end experiments were devised, and were carried out by making alternate hauls with the cod-end in question and the same cod-end fitted with a shrimp netting cover, the combined catches of the latter being used to obtain an index of the population frequency within the selection range. For this reason they were less satisfactory than the four later experiments discussed in detail above, but were adequate to establish approximately the

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*Mr. B. B. Parrish has informed us that the shoaling behaviour of the whiting (*Gadus merlangus*) may present difficulties in this connection.

†In so far as the greater catches of the larger-meshed nets were due to their greater efficiency it is to be expected, as mentioned in §8.1.1.1, that the latter would be caused by the faster flow of water through the larger meshed cod-end and the reduced resistance of the net to towing. If we postulate that the larger the fish the greater is its ability to swim against such a water flow, then we should expect the greater efficiency of the larger-meshed trawl to become progressively less pronounced for fish of larger sizes. This is a possible reason for the descending regressions of meshes 72.2 mm. and 113.0 mm.

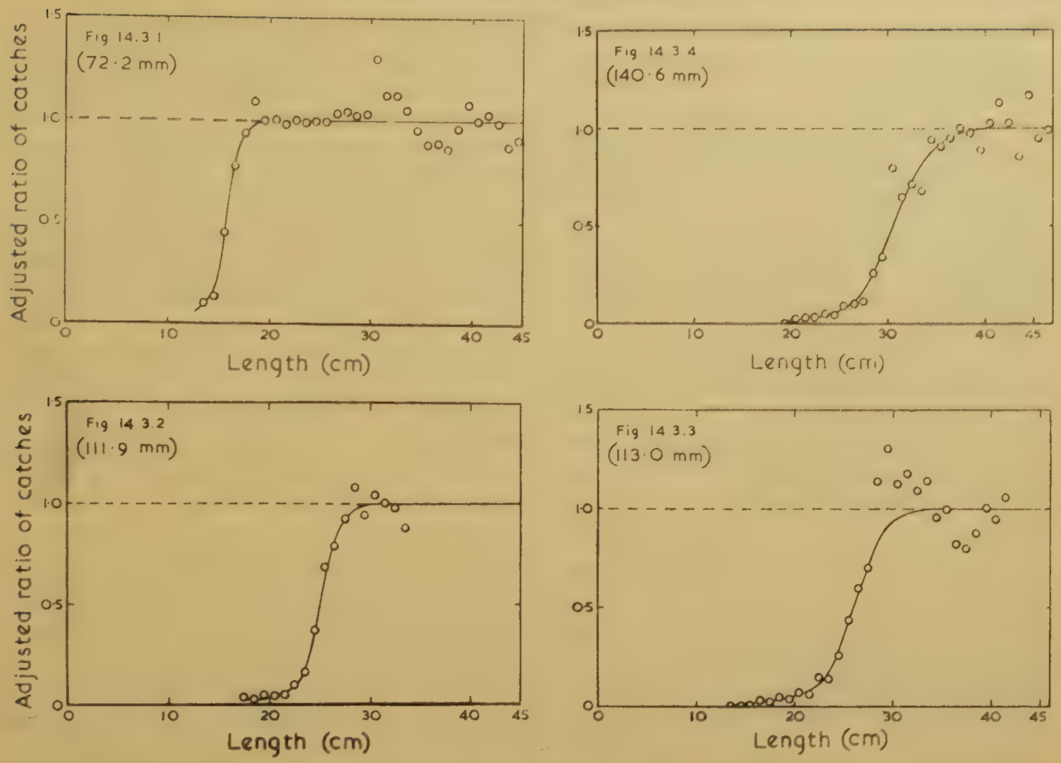

FIG. 14.3 PLAICE MESH SELECTION

[The selection curves shown in Fig. 14.2 are here adjusted by methods described in the text so that in each case they approach an upper asymptote of unity. The length at which these ogives have an ordinate of 0.5 is the 50% selection length for the mesh in question (see Fig. 14.4).]

positions of the selection points, though not always of the shapes of the ogives. We have therefore included these observations in Fig. 14.4, in which are plotted the 50% selection points against mesh size for each of the eleven different cod-ends investigated, the four cod-ends discussed in detail above being indicated by solid circles. It will be seen that the points are fitted well by a straight line passing through the origin, the equation being

$$50\% \text{ selection length} = 2.18 \times \text{mesh size}$$

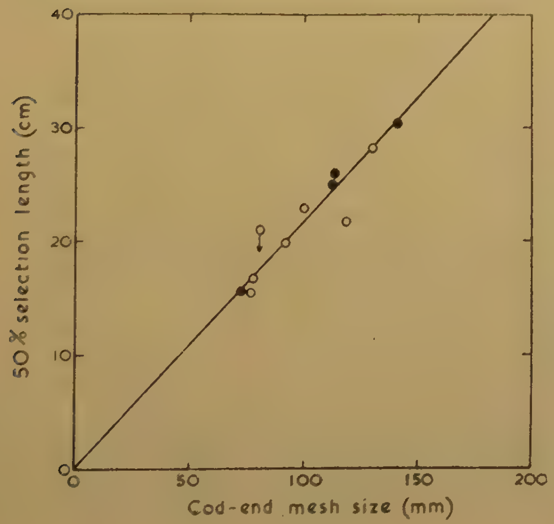

FIG. 14.4 PLAICE MESH SELECTION

[Relationship between 50% selection length and cod-end mesh size. Solid circles refer to the selection ogives of Fig. 14.3, hollow circles to estimates obtained from other experiments not discussed in full here. The point ♀ was known to be less than 21 cm. but its actual value could not be determined owing to the scarcity of small fish. It will be noted that the relationship is closely proportional, and gives an estimate of the selection factor $b = 2.18$.]

Hence our estimate of the selection factor for plaice is 2.18. Jensen (1949), from a study of published data on plaice mesh experiments based mainly on the covered cod-end method, deduced a similar value, viz.: 2.1. It should be noted that this estimate refers to double twine cod-ends of trawls, as does our use of the term 'mesh size' in later parts of this paper.

In addition to establishing the relation between cod-end mesh size and 50% selection length we need also to obtain some measure of the spread of the ogives, though this problem raises several difficulties. It is not possible to establish with precision the shape of the upper halves of the ogives shown in Figs. 14.3, but the indication is that they are not symmetrical, and, in particular, that the lower tails approach zero more slowly than would be expected if the ogives were normal curve integrals as suggested by Buchanan-Wollaston (1927). Nevertheless, the superficial resemblance is sufficiently close to use a normal ogive as a convenient means of representing the spread of a selection curve until a more detailed analysis can be undertaken. As a measure of the spread of the curves of Figs. 14.3 we have therefore read off the 25% and 75% selection lengths, and by using the value of x/σ of a normal curve at these percentages obtained a value of σ for each mesh. These are given in column C of Table 14.11, and it will be seen that there is a definite tendency for spread to increase with mesh size.

14.2.2 *Haddock—parallel hauls with meshes having overlapping selection ranges*

We may at this point leave plaice and pass on to the problem of the derivation of cod-end selection ogives for haddock. As far as the authors are aware, no mesh experiments using the alternating haul method have been carried out with this fish. On the other hand, Davis (1934) gives the results of a commercial mesh experiment on haddock carried out by two sister trawlers working from N. Shields. Over four hundred hauls were made, giving a detailed comparison of the length distribution of the catches of a trawl fitted with a normal cod-end of the mesh size then in general use (23.70 rows/yd.), and a similar trawl fitted with a cod-end of a rather larger mesh, (20.73 rows/yd.). The number caught at each length per 100 hours fishing by the 'normal' and 'abnormal' cod-ends from Table IV of Davis (columns (4) and (5)) are given in columns A and B of Table 14.12.

The first point to note, as stressed by Davis, is that the catches of the larger fish by the abnormal cod-end are greater than by the normal, as was found in most of the plaice experiments. Our estimate of these increased catches in Davis' data was obtained by summing the catches of the normal and abnormal cod-ends of fish of 33 cm. and above, at which point it seemed that the selection range of both meshes was safely passed. The ratio thus obtained was 1.272 in favour of the abnormal cod-end, and column C gives the adjusted catches by the abnormal cod-end obtained by dividing column B by this factor.

By plotting the data given by Davis for double tarred manilla twine (Table XVI, columns IX and XI, samples 7-12 inclusive), we find that the 23.70 rows/yd. of the normal meshed cod-end corresponds to an internal mesh measurement of 70.5 mm. while the abnormal mesh with 20.73 rows/yd. had an internal measurement of 83.0 mm. This difference between the two cod-ends is so small that their selection ranges might be expected to overlap. Consequently, the ratio of the catches at each length by the larger-meshed cod-end to the smaller (column D of Table 14.12) shown in Fig. 14.5 cannot now be relied on to provide a direct estimate of the selection ogive of the larger mesh or its true 50% selection point. As Davis pointed out, the latter must be greater than the length at which the larger mesh catches half the number caught by the smaller mesh (27.0 cm.), since the catches of the small mesh are themselves underestimates of the relative population frequencies over the selection range of the larger mesh. Despite this, an estimate of the true 50% selection point of both cod-ends can be obtained in the following way.

Suppose that the ratio of the catches of fish of a certain length per unit fishing time by the two meshes is q_2/q_1, where q_2 refers to the larger mesh, and is therefore less than q_1 within the selection ranges. If p is the true relative population frequency at this length, which would have been observed if a much smaller mesh had been used, then q_1/p and q_2/p are the true selection ratios for fish of this length for each mesh respectively. Dividing the second of these ratios by the first again gives the quantity q_2/q_1. In other words, taking

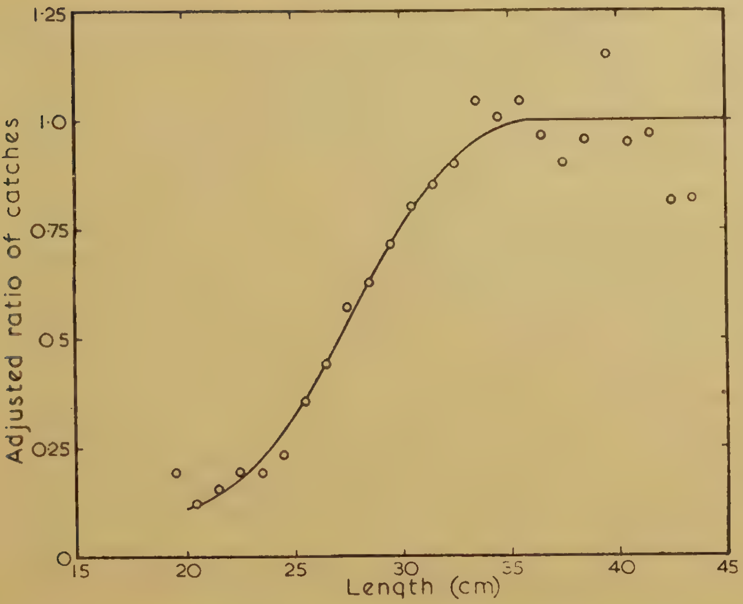

FIG. 14.5
HADDOCK MESH SELECTION

[Ratios of numbers caught per unit fishing time by 'abnormal' (83 mm.) to 'normal' (70 mm.) meshed cod-ends plotted against length of fish and adjusted to an upper asymptote of unity; from Table 14.12, column D. The selection ogives of these two meshes partly overlap and the true 50% selection length of the larger mesh is about 0.7 cm. greater than that indicated in the figure (see text and Fig. 14.6).]

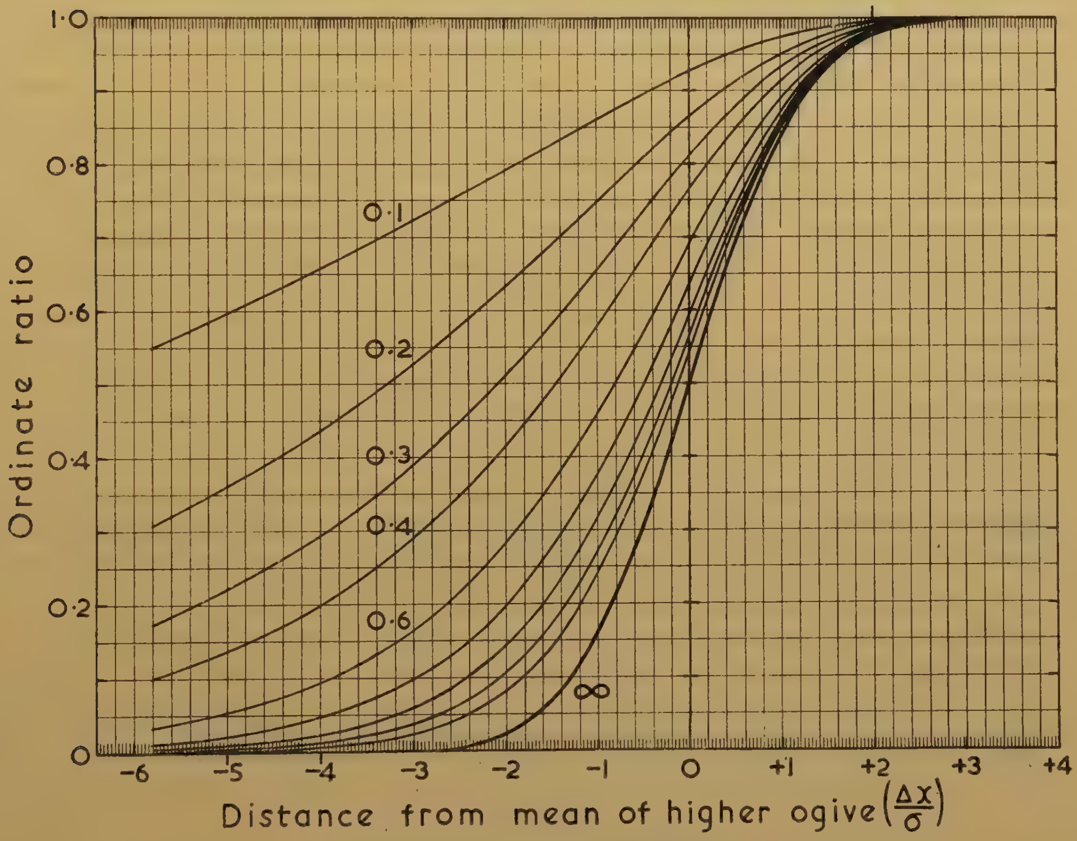

FIG. 14.6 OGIVE RATIO CURVES

[Ratios of ordinates of pairs of normal curves having the same standard deviation but with means displaced by various amounts. The figures shown against some of the ratio curves denote the displacement of the means, as ratios of the standard deviation. Above a displacement of 0.6 the curves are too close to label in this way but continuing downwards from the labelled curves they are 0.8, 1.0, 1.2, 1.4 and ∞ (thickened). Matching these theoretical ogive ratio curves with the curve of Fig. 14.5 provides a method of estimating the true 50% selection length of the latter (see text.)]

ratios of the two catches at each length gives a curve identical to that which would have obtained by dividing the true selection ogive of the larger mesh by that of the smaller.

Now the two mesh sizes in the Shields experiment were so similar that the spread of their true ogives is unlikely to differ appreciably, and it seems permissible to assume equality. Furthermore, it will serve the present purpose to assume that the true selection ogives can be represented by the integrals of two normal curves having different means but the same standard deviation. Fig. 14.6 shows graphs of the ratios of the ordinates of pairs of such normal ogives whose means are displaced by various proportions of their standard deviation, i.e. for various values of $\Delta\bar{x}/\sigma$. The numerator of these ratios is the ordinate of the higher ogive and the denominator is that of the lower ogive, and they are plotted against distance from the mean of the higher ogive as a ratio of the standard deviation ($\Delta x/\sigma$). When $\Delta\bar{x}/\sigma =$ zero the two ogives are coincident and all ratios are therefore unity; at the other extreme, as $\Delta\bar{x}/\sigma \to \infty$, the ogives are displaced so far that the lower has effectively reached its asymptote at unity over the important range of the higher ogive, so that the ratio curve is the higher ogive itself. This is shown by the thickened curve in Fig. 14.6. At intermediate values of $\Delta\bar{x}/\sigma$ the ratio curves are asymmetrical and their shape changes rapidly as $\Delta\bar{x}/\sigma$ is increased from zero, although when $\Delta\bar{x}/\sigma$ has reached about 1.5 the ratio curve is virtually indistinguishable from the upper ogive. If, now, we find which ogive-ratio curve of Fig. 14.6 is most similar in shape to the curve of Fig. 14.5 we can estimate the displacement of the true ogives of each mesh used in the Shields experiment and, furthermore, estimate the true 50% point of each and their standard deviation.

A measure of shape that is sufficiently accurate for the present purpose can be obtained by reading off values of the abscissa x_1, x_2 and x_3 at ordinates 0.25, 0.5 and 0.75, and computing the ratio

$$\frac{x_1 - x_2}{x_2 - x_3}$$

For the observed curve of Fig. 14.5 we find

$$x_1 = 23.90 \text{ cm.}$$

$$x_2 = 27.10 \text{ cm.}$$

$$x_3 = 29.90 \text{ cm.}$$

so that

$$\frac{x_1 - x_2}{x_2 - x_3} = 1.143$$

This value agrees most nearly with that derived from the curve of Fig. 14.6 for a difference between means of 1.2σ; thus for this curve, and denoting the abscissae $\Delta x/\sigma$ by x', we have

$$x_1' = -1.10$$

$$x_2' = -0.20$$

$$x_3' = 0.58$$

giving

$$\frac{x_1' - x_2'}{x_2' - x_3'} = 1.154$$

It can be seen at once that the theoretical ratio curve for $\Delta\bar{x}/\sigma = 1.2$ does not differ much from the upper ogive, from which it follows that the curve of Fig. 14.5 obtained by dividing the catches of each mesh is not much different from the true ogive of the larger mesh. The position of the true 50% point of the latter can be estimated from the fact that the ratio curves of Fig. 14.6 have been plotted so that the origin at $x' = 0$ corresponds to the

50% point of the higher of the two ogives. Thus at the origin it is seen that the curve for $\Delta\bar{x}/\sigma = 1.2$ crosses the Y – axis at a value 0.57; hence it follows that the 50% selection length of the true ogive of the larger mesh is the value on the X – axis at which the curve of Fig. 14.5 reaches 0.57 on its Y – axis, namely 27.7 cm. The true 50% point of the larger mesh is therefore about 0.7 cm. higher than the apparent 50% point obtained from direct ratios of the catches.

The 50% selection length of the smaller mesh is arrived at by first computing the difference between the 50% selection lengths of the two meshes. Remembering that the abscissae (x') of Fig. 14.6 define the ratio of the difference from the 50% point of the larger mesh to the standard deviation, whereas the abscissae (x) of Fig. 14.5 are in absolute units of length, it follows that the standard deviation of the actual ogives is given by

$$\sigma = \frac{x_1 - x_3}{x_1' - x_3'} = \frac{6.00}{1.68} = 3.57 \text{ cm.}$$

Hence the difference between the means of the actual ogives in centimetres is

$$1.2 \times 3.57 = 4.3 \text{ cm.}$$

so that the 50% selection length of the smaller mesh is

$$27.7 - 4.3 = 23.4 \text{ cm.}$$

These estimates for the two meshes give an almost exactly proportional relationship between 50% selection length and mesh size (see §14.2.3), with a selection factor of $b = 3.33$. This value is somewhat higher than that usually found in covered cod-end experiments, viz. 2.9 (see Davis (1934) and Jensen (1949)) and Davis regarded this as due to the 'masking' effect of the cover.* There are, however, two other factors that might cause the 50% point of a covered cod-end to be too low. One is that some fish may return to the cod-end after having previously escaped through it to the cover, perhaps mainly while the net is lying alongside after being hauled. The other arises from the practical difficulty of fitting a loose cover to the underneath of a cod-end: if this part of the cod-end is lined internally with cover-netting, as in Davis' experiments, some fish that would otherwise have escaped may not do so; while if no small-meshed netting is attached at all the cover will not retain any that escape from the underside of the cod-end, so that the combined catches in the cod-end and cover will give an underestimate of the true population frequencies in the selection range. All these factors would tend to make ratios of the catch in the cod-end to the catch in the cod-end plus cover over the selection range too high, and it seems quite reasonable to suppose that their combined effect could cause the difference between selection factors noted above. For this paper we shall therefore use a selection factor of 3.33 for haddock, this referring to double tarred cod-ends of trawls.

The ogive-ratio method discussed above was developed in the first instance to make use of the data of the North Shields experiment, which is unique in the large number of parallel hauls that were made, but the method has one particular advantage which is worth noting. It will be seen from Fig. 14.6 that the shape of the ogive-ratio curves changes most rapidly with $\Delta\bar{x}/\sigma$ at values of the latter below unity, and hence that the catches of two meshes more similar than those used in the Shields experiment could be analysed in this way to give estimates of the true 50% point of each. This means that any systematic errors due to the effect of different sized cod-ends on the fishing behaviour of the trawl as a whole are kept to the minimum. On the other hand, the method does not give the shape of a selection ogive, and may lead to errors if the true selection curves of the two meshes depart appreciably from normal curve ogives. These considerations suggest that mesh selection experiments might with advantage take the form of alternate hauls with cod-ends of three sizes, one of which is small enough to retain all fish within the selection ranges of the two larger meshes, these latter differing only slightly in size, say between 5 and 10 mm. in the case of haddock. Comparison of the catches of the two larger meshes with those of the smallest mesh as in §14.2.1, and with each other as described above, would provide an estimate of the shape of the selection ogives of the two larger meshes and also two partially independent and 'complementary' estimates of their 50% points.

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*Since the above was written, a preliminary report on recent mesh selection experiments on the Georges Bank haddock using the covered cod-end method has been published (Clark, 1952). The two cod-end meshes tested, of 95 mm. and 105 mm., gave selection factors of 3.36 and 3.39 respectively. H. W. Graham (1952) has prepared a diagram illustrating the fit to various selection data for haddock of the regression obtained with the selection factor of 3.33 deduced here.

14.2.3 *Some factors influencing gear selectivity*

Further evidence on selection can be obtained by considering certain of the factors responsible for the location and spread of a selection ogive. Whether or not a fish of a given species and size can escape through a given mesh clearly depends, *inter alia*, on the shape of the cross-section of the fish and the mesh lumen, and on the relative magnitudes of the maximum girth of the fish and the internal perimeter of the mesh lumen. It is reasonable to suppose that the 50% selection length bears some simple relationship to the length of a fish that just fits the mesh, and it is interesting and may be of practical importance to find, by taking this criterion, how close an approximation could be obtained to the relationships between 50% selection length and mesh size given above.

Measurements of length and maximum girth of ungutted plaice and haddock covering the selection ranges of the experimental meshes are summarised in Table 14.13, the relationships between them being shown graphically in Fig. 14.7. It will be seen that maximum girth and length are closely proportional within the range of the data in both species, which is in harmony with our previous finding that 50% selection length and mesh size are proportional in these fish. The mean length/max. girth ratios were found to be 1.18 in the plaice and 1.97* in the haddock.

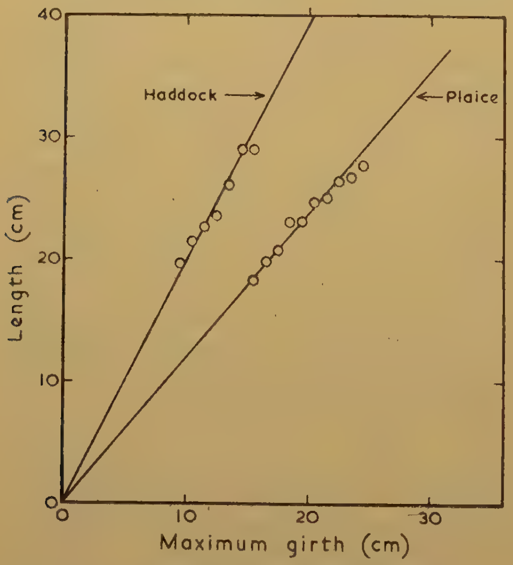

FIG. 14.7 RELATIONSHIP BETWEEN LENGTH AND MAXIMUM GIRTH IN PLAICE AND HADDOCK

[In each case the trend is closely proportional within the range of lengths involved in the selection experiments described previously.]

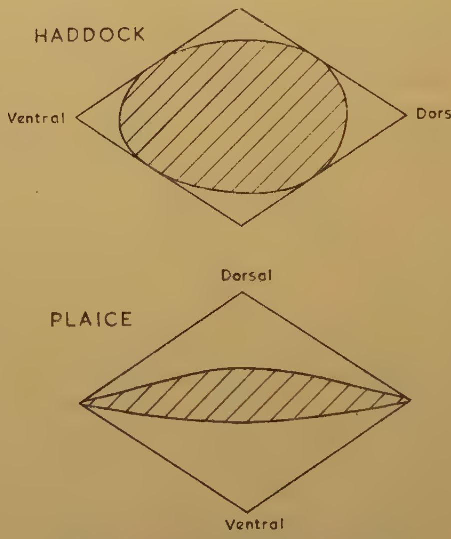

FIG. 14.8 GIRTH AND MESH SIZE IN PLAICE AND HADDOCK

[Cross-sectional diagrams at the point of maximum girth are shown enclosed by a rigid mesh lumen having axes in the ratio 3 : 2. These diagrams give a rough measure of the ratio of maximum girth to size of mesh that just fits each species of fish.]

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*This figure is virtually identical with that obtained from length-girth measurements, covering a wider range than our own, kindly sent to us by Mr. R. Jones of the Marine Laboratory, Aberdeen, who also concluded independently that the order of the difference between the selection factors for plaice and haddock could be explained from the difference between their girth-length ratios. Further data on the relation between length and girth in haddock have since been published by Margetts (1954) and Lucas *et. al.* (1954).

The internal perimeter of a mesh lumen is of course simply twice the mesh size, as measured in the usual way using a flat gauge. However, although all four sides of the mesh are the same length, the net is braided in such a way that the meshes tend to take up a diamond shape, with one axis longer than the other; the extent to which the shape of the lumen departs from square must have an important bearing on the size of fish that can escape through, especially for plaice. Measurements of the shape of the lumen in the cod-end when the gear is being towed, in terms of the ratio of the two axes of the diamond, have been obtained from photographs taken from the Ministry's film "Trawls in Action", kindly placed at our disposal by our colleague Mr. A. R. Margetts. From these it was apparent that the shape of the diamond depends to some extent on the weight of fish in the cod-end, the greater this is the more nearly square it becomes. It was found that the ratio of the long to short axes of the diamond varied from 4 : 3 to 2 : 1, the most usual ratio being about 3 : 2.

In Fig. 14.8 are therefore shown drawings of a mesh with the axes in the ratio 3 : 2, together with a simplified drawing of the cross-section of a plaice and a haddock of sizes which just fit. These drawings were constructed from measurements of fish cut transversely at the point of maximum girth; they are, admittedly, approximate only, but the exact shape is not critical. Even a difference in shape as marked as that between plaice and haddock results in a relatively small difference in the ratio of girth to mesh size, as can be seen from the fact that measurements of these diagrams gave estimates of the max. girth/mesh size ratios of 1.69 in plaice and 1.56 in haddock.

The relationships between 50% selection length and mesh size predicted in this way are therefore

$$\begin{aligned}50\%\text{ selection length} &= 1.69 \times 1.18 \times \text{mesh size}\\ &= 1.99 \times \text{mesh size}\end{aligned}$$

for plaice, and

$$\begin{aligned}50\%\text{ selection length} &= 1.56 \times 1.97 \times \text{mesh size}\\ &= 3.06 \times \text{mesh size}\end{aligned}$$

for haddock. It will be noted that the selection factors obtained in this way are quite similar to those obtained previously from mesh experiments. More important is that each is lower by almost exactly the same proportion, i.e. about 8%, which perhaps supports our use of the value 3.33 for the haddock in preference to the somewhat lower values given by covered cod-end experiments. The difference is in the direction that might be expected, since in measuring girth no tension was exerted to deform the fish, whereas an actively struggling fish can probably 'squeeze' through a slightly smaller mesh than is indicated by the diagrams of Fig. 14.8. Some deformation of the mesh itself may also occur, especially with plaice. Furthermore, there is bound to be some variation in the size of mesh within one cod-end (see below), and fish just too small to escape through the smaller meshes may do so through the larger ones after several attempts. Thus the effective mesh size may be rather greater than the mean size of mesh in the cod-end. A combination of these factors could easily account for the difference between the observed selection factors and those predicted by the method described above.

The factors responsible for the *spread of a selection ogive* are less susceptible to analysis than are those determining the 50% selection point; there are at least two, however, that can be distinguished and measured, namely the variation in length of fish of a given girth, and the variation in mesh size within the cod-end in question. For plaice it has been possible to obtain a maximum estimate of the fraction of the observed spread of the selection ogives of Figs. 14.3 that can be attributed to these two factors.

In column D of Table 14.13 is given the standard deviation of length of fish in each centimetre girth-group of column A, and in Table 14.14 are given estimates of the standard deviation of mesh size within each of the cod-ends used in the selection experiments described in §14.2.1. There is a slight tendency for the latter to increase with mesh size, but for the present purposes it is sufficient to use mean values. Thus the mean variance due to the variation of length at a given girth is:

$$\sigma^2 = 1.00 \text{ cm.}^2$$

while that of mesh size is

$$\sigma^2 = 0.10 \text{ cm.}^2$$

The latter needs to be expressed in terms of length, which can be done using the factor for plaice deduced above, so that

$$\sigma^2 = 0.10 \times 1.99^2 = 0.40 \text{ cm.}^2$$

Hence the total variance from these two sources, in terms of length of fish, is

$$\sigma^2 = 1.00 + 0.40 = 1.40 \text{ cm.}^2$$

Now the average spread of the four selection ogives of Figs. 14.4 is 5.1 cm.^{2}, so that the two factors in question can account at the most for about 27% of the observed variance.*

These considerations suggest that a working estimate of the 50% selection length of a given mesh can be obtained from a knowledge of the shape and maximum girth of the fish in question, provided of course that the latter does not possess projecting spines, etc., that could entangle in the meshes (Van Oosten, 1935), and is not able to deform its shape excessively in squeezing through the net. On the other hand, only about one-quarter of the observed spread of the selection ogive in the case of plaice can be accounted for in terms of factors that are open to direct measurement. The greater part of the spread must therefore be due to variation in the activity of the fish and to the possibility that some fish within or below the selection range may be damaged or even killed by the trawl, and hence unable to escape; that the shape as well as the size of mesh in a cod-end varies; and that the process of selection may not be complete when the catch is examined.

14.2.4 *The overall selectivity of a net*

The selection ogives obtained by the experimental methods described in §§14.2.1 and 14.2.2 will be true for the cod-end, but only if there is no escape from any other part of the trawl will its mean selection length be the value of $L_{\rho'}$ that is needed in exploitation equations. The absence of any precise information on this point has made it necessary for us to ignore this factor at present, but certain workers (e.g. Todd, 1911, and Borowik, 1930), by attaching covers to various parts of the trawl, have shown that a small amount of selection does occur other than in the cod-end. Since further experiments using the same technique have recently been carried out from the Aberdeen and Lowestoft laboratories, it is appropriate to conclude this discussion of mesh selection with a note on how the method could be used to obtain the true selection ogive of the trawl as a whole.

Let us suppose that we wish to determine the true selection curve of a trawl having a cod-end of a given size, the selection curve of the latter having been previously determined. Let q be the number of fish at a certain length caught per unit fishing time by this trawl fishing on a given population, and let p be the true population frequency at this length, so that we may define the total selection ratio, that is, for the trawl as a whole, as

$$y = \frac{q}{p}$$

---

*This figure is, if anything, an overestimate, since the mesh sizes and girths are likely to have a bigger 'measurement error' than the lengths from selection experiments. Repeated measurements of the girth of four plaice of slightly different sizes, presented in a random order to the measurer so that he could not anticipate the girth measurement, gave a mean variance of 0.044 cm.^{2}, i.e. 3% of the total variance of 1.40 cm^2. The error variance of the mesh data is not known, but it is possible that the total variance figure quoted above may be 5% to 10% too large as a result of measurement errors of both kinds.

A cod-end mesh experiment would provide an estimate of the cod-end selection ratio at this length, say y', where

$$y' = \frac{q}{p - r}$$

and r is the number of fish at that length that escape from parts of the net other than the cod-end during the experiment.

Suppose now that a small-meshed cover is attached in turn to various typical parts of the net, and the catches obtained in the cover when in the various positions are noted. By observing the distribution of these values over the trawl it should be possible to arrive at an estimate of the total number of fish, s, which would have been caught in a large cover attached to the whole of the rest of the trawl apart from the cod-end.* We can use s as an estimate of r though it might be, to a slight extent, an underestimate if any fish go back into the trawl from the cover after having once escaped. Hence we can put

$$y' = \frac{q}{p - s}$$

so that

$$p = \frac{q}{y'} + s$$

and

$$y = \frac{q}{q/y' + s}$$

which is the required estimate of the total selection ratio at this length.†

Since y' must always be greater than y, the mean selection length for the cod-end will also be less than that for the whole trawl, irrespective of the size of the mesh in the rest of the trawl. We would, however, expect that the amount of escape in parts other than the cod-end is relatively small, if only because such escape must be effected during the relatively short time between fish entering the mouth of the trawl and reaching the cod-end.

14.3 Separate Estimation of Fishing and Natural Mortality Coefficients from Age-Composition Data

When discussing estimation of the total mortality coefficient $(F + M)$ from age-composition data in §13.1, we gave a general equation for the ratio of the abundance of a given year-class in any two consecutive years of life (13.4). In the present section we consider F and M separately and are concerned with separating the total mortality coefficient into these two components.

From our study of the methods of analysis of marking experiments, we concluded that only in rather exceptional circumstances would it be possible to obtain reliable estimates of the natural mortality coefficient in this way, owing to the existence of other losses which may be considerably greater than natural deaths, and not all of which can be assessed. The value of marking experiments in this connection is that they can provide, in suitable circumstances, good estimates of the absolute value of F, of its change with age and of the constant c which relates F to the fishing intensity. One method of estimating M is therefore to subtract F estimated in this way from the total mortality coefficient. This procedure does not require a separate theoretical discussion and is considered with reference to data for plaice in §14.3.2.1.

In many instances it may be impossible for various reasons to conduct a marking experiment that can give a reliable estimate of F. It is therefore important to discuss a method by which the total mortality coefficient can be separated into its components—with no additional information other than a knowledge of the fishing intensity, provided the latter varies over an adequate range during the period to which the age-composition data refer. We establish the theoretical basis of this method in §14.3.1 and give some examples of its application in §§14.3.2.2 and 14.3.2.3.

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*It will be appreciated that the actual use of such a large cover, or for that matter of a small-meshed trawl, would involve practical difficulties and would probably interfere unduly with the normal fishing of the trawl.

†This method does not of course take account of any differential escapement from the mouth of the trawl, a problem which is discussed in §8.1.2.

14.3.1 *Theoretical*

For our basic equation we refer again to (13.4) and restate it in a form which distinguishes the particular values of F and M in each year and the age-groups in question, viz.:

$$\log\left(\frac{{}_{\theta}\bar{N}_X}{{}_{\theta+1}\bar{N}_{X+1}}\right) + \log\left\{\frac{(F_X + M_X)\,(1 - e^{-(F_{X+1} + M_{X+1})})}{(F_{X+1} + M_{X+1})\,(1 - e^{-(F_X + M_X)})}\right\} = F_X + M_X \quad .. \quad (14.85)$$

where ${}_{\theta}\bar{N}_X$ is the mean abundance of age-group θ in year X, and ${}_{\theta+1}\bar{N}_{X+1}$ that of age-group $(\theta + 1)$ in year $(X + 1)$ (and hence refers to the same year-class); F_X, M_X and F_{X+1}, M_{X+1} are the fishing and natural mortality coefficients in the two years respectively. It can be seen that even if F_X and F_{X+1} are known (e.g. from marking experiments) we cannot obtain solutions for both M_X and M_{X+1} from (14.85); moreover, we are primarily concerned with the case in which we do not know the absolute value of F but only the effective overall fishing intensities $\bar{f}_X$ and $\bar{f}_{X+1}$, as defined in §10.2.3.

Let us suppose for the moment that we can assume the value of M to be the same in both years and for both age-groups. Putting also

$$F_X = c\bar{f}_X$$

and

$$F_{X+1} = c\bar{f}_{X+1}$$

(14.85) can be written as

$$\log\left(\frac{{}_{\theta}\bar{N}_X}{{}_{\theta+1}\bar{N}_{X+1}}\right) + \log\left\{\frac{(c\bar{f}_X + M)\,(1 - e^{-(c\bar{f}_{X+1} + M)})}{(c\bar{f}_{X+1} + M)\,(1 - e^{-(c\bar{f}_X + M)})}\right\} = c\bar{f}_X + M \quad .. \quad (14.86)$$

This equation will be recognised as analogous to (14.19), and solutions for c and M can be obtained in a similar way. Thus putting the second logarithmic term to zero gives the linear equation

$$\log\left(\frac{{}_{\theta}\bar{N}_X}{{}_{\theta+1}\bar{N}_{X+1}}\right) = c\bar{f}_X + M \qquad .. \quad .. \quad .. \quad (14.87)$$

which is analogous to the linear relationship (8.36) deduced from first principles in §8.3.1. As in the case of (14.19), a minimum of three successive estimates of abundance are required to obtain separate solutions for c and M, and in the general case we shall have data from a number of years which can be treated graphically. Thus plotting logarithms of the ratios of abundance against the fishing intensity in the first of each pair of years and fitting the linear regression gives first estimates of c (slope) and M (intersect). Using these values to compute the whole of the left hand side of (14.86) and replotting against $\bar{f}_X$ enables a second regression to be fitted which provides more accurate values of c and M, and the process is continued until successive estimates of c and M are sufficiently similar.

Certain modifications of the above method may be noted at this point. Depending on the accuracy of the age-composition data, it may be necessary to use all age-groups in the exploited phase to estimate the ratio of abundance in each pair of years; there is no objection to this procedure except that it precludes the possibility of investigating whether the natural mortality rate changes with age, a problem discussed below. A special case of (14.86) arises if the fishing intensity has been stabilised at two different levels which we may denote by the suffixes ${}_A$ and ${}_B$, each level covering a period of at least two years. Since $\bar{f}_X = \bar{f}_{X+1}$ during each steady state, we can denote the two levels of fishing intensity by $\bar{f}_A$ and $\bar{f}_B$ respectively, and for steady state A we have from (14.86)

$$\log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_A = c\bar{f}_A + M$$

and for steady state B

$$\log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_B = c\bar{f}_B + M$$

the logarithmic terms referring to the ratios of abundance of successive age-groups in the two steady states. From the above equation we have

$$c = \frac{1}{\bar{f}_A - \bar{f}_B}\left\{\log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_A - \log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_B\right\} \quad .. \quad (14.88)$$

and

$$M = \frac{1}{\bar{f}_B - \bar{f}_A}\left\{\bar{f}_B \log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_A - \bar{f}_A \log\left(\frac{_\theta\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right)_B\right\} \quad .. \quad (14.89)$$

Silliman (1943) used what is essentially the same procedure to estimate natural mortality in the Californian sardine, and in §14.3.2.2 we illustrate the above method by applying it to his data. If the fishing intensity should be zero for a period of two years or more the logarithmic term gives, of course, an immediate estimate of M, and this is how M for the plaice has been obtained in §14.3.2.3.

In the above methods the natural mortality coefficient is assumed to remain constant; we must now examine the consequences of variation in this parameter and methods for estimating it. If the variation in M is uncorrelated with the fishing intensity, the intersect of the regression fitted to (14.86) gives an estimate of the mean natural mortality coefficient during the period covered by the age-composition data. In these circumstances the deviations of individual points from the fitted regression provide an approximate measure of the extent to which individual values of M differ from the mean, after allowance has been made for sampling variation of the age-composition data.

This procedure is satisfactory if the variation in M is due to factors external to the population itself, such as environmental conditions. If, however, the natural mortality rate varies with density, its magnitude will tend to be correlated with the fishing intensity. The same is true if M varies with age and all age-groups in the exploited phase are used to estimate a mean ratio of abundance, since the mean age of fish will also be correlated with the fishing intensity. Apart from the importance of knowing how M varies with age and density from the point of view of assessing the probable behaviour of the population, the presence of such variation will mean that the regression used to fit (14.86), and hence the estimates of c and M, will be biased. It is therefore necessary to discuss a possible approach to the problem when M varies in this manner.*

For the general case in which M varies with both age and density we can regard its values as lying on a surface defined by the co-ordinates of age and density. In the first instance we can suppose that M increases linearly with age at a given density, and linearly with density at a given age (see §§7.2 and 7.3), so that the surface is a plane. The natural mortality coefficient for fish of age-group θ in the year x when the density is $(\bar{P}_N)_X$ can then be defined by the equation

$$_\theta M_X = M_0 + m\theta + \mu(\bar{P}_N)_X \quad .. \quad .. \quad .. \quad (14.90)$$

---

*In an analysis of data of total mortality and effort for the California Sardine fishery, Widrig (1954) has shown that the regression of apparent total mortality coefficient on effort may also be biased when there is 'partial availability', that is, when the fishing activity is distributed over part of the fishable population only (see §10.2.2). The author shows that in this case the relation between apparent total mortality coefficient (as estimated from catch samples taken from the fished area) and effort is curvilinear, tending towards an asymptote as effort increases, and discusses the influence of varying degrees of availability on the estimation of total population size and the natural mortality rate. For a further discussion of this and other problems of special relevance to pelagic fisheries, the reader is referred to the author's original paper.

and for age-group $\theta + 1$ in the year $X + 1$ we have

$$_{\theta+1}M_{X+1} = M_0 + m(\theta + 1) + \mu(\bar{P}_N)_{X+1} \quad \ldots \quad \ldots \quad (14.91)$$

Although independent solutions for $_{\theta}M_X$ and $_{\theta+1}M_{X+1}$ cannot be obtained from (14.86) as it stands, we can now write this equation in the form

$$\log\left(\frac{_{\theta}\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right) + \log\left\{\frac{(c\tilde{f}_X + {_{\theta}M_X})(1 - e^{-(c\tilde{f}_{X+1} + {_{\theta+1}M_{X+1}})})}{(c\tilde{f}_{X+1} + {_{\theta+1}M_{X+1}})(1 - e^{-(c\tilde{f}_X + {_{\theta}M_X})})}\right\} =$$

$$= c\tilde{f}_X + M_0 + m\theta + \mu(\bar{P}_N)_X \quad \ldots \quad \ldots \quad (14.92)$$

which provides the basis for a more detailed analysis of age-composition data using the same iterative method as before. Thus putting the second logarithmic term to zero gives the equation

$$\log\left(\frac{_{\theta}\bar{N}_X}{_{\theta+1}\bar{N}_{X+1}}\right) = c\tilde{f}_X + M_0 + m\theta + \mu(\bar{P}_N)_X \quad \ldots \quad \ldots \quad (14.93)$$

and first estimates of the parameters it contains may be determined by a multiple regression analysis. These can then be used to compute the whole of the left hand side of (14.92) and the analysis repeated to obtain more exact estimates of c, M_0, m and μ. In practice it might be possible to use simpler modifications of this procedure, depending on the form of the data. For example, if the exploited phase of the population contains a number of age-groups, the difference between the densities in successive years may be small enough to enable the data to be grouped into two or more periods within each of which the density changes can be ignored. In this case we can put

$$_{\theta}M_X = m_0 + m_1\theta$$

$$_{\theta+1}M_{X+1} = m_0 + m_1(\theta + 1)$$

in (14.92). The values of m_0 and m_1, which will differ for each period, can then be examined for variation with density.

The principle on which the methods of this section are based is simply to measure the changes in the total mortality coefficient caused by a given change in fishing intensity; the more nearly these changes are in the same proportion, the smaller must be the residual mortality due to natural causes, and vice-versa. A necessary requirement is therefore that the changes in fishing intensity should be estimated with sufficient accuracy, and, moreover, should be large enough to produce a change in the total mortality coefficient which can be distinguished from sampling variations (see §14.3.2.2). Another possible way in which the method might be applied is to use a knowledge of the relative change in the fishing mortality coefficient with age due to the selective characteristics of the gear, which could be obtained from gear selection experiments. A limitation of this method is, of course, that it provides an estimate of the natural mortality coefficient only for those age-groups within the selection range.

The method of treating age-composition and fishing intensity data used by Schuck (1949) may be mentioned here, since it is related to that described above. His main objective was to show that variations in size of the Georges Bank haddock population were reflected in the variations in the yield, and to this end he plotted estimates of the total annual decrease in stock weight against the corresponding yield. Because the regression passed nearly through the origin, Schuck concluded tentatively that the natural mortality was very small, at least, under conditions of heavy fishing. However, a regression obtained in this way will be generated partly by natural fluctuations in population size (e.g. those caused by fluctuations in recruitment); since these affect more or less proportionately both population decrease and catch, they tend to make the regression pass through the origin.

If recruitment was exactly constant over the period in question, a regression of population decrease on catch would be due entirely to changes in fishing intensity, and its intercept on the population decrease-axis would be a measure of the average number of fish dying from natural causes each year; in this case, however, the regression would not be linear.

It will be noted that a consequence of using data of the annual mean abundance of age-groups is that values of parameters in at least two consecutive years enter into a determination of those in any one year. There is therefore the possibility that comparison of estimates of abundance for pairs of months one year apart might be advantageous in some cases (see Jones, 1956). By treating these estimates as effectively instantaneous, the general equation analogous to (14.86) would then become

$$\log\left(\frac{{}_{\theta}N_X}{{}_{\theta+1}N_{X+1}}\right) = c\bar{f}_X + M_X \quad .. \quad .. \quad .. \quad (14.94)$$

where ${}_{\theta}N_X$ and ${}_{\theta+1}N_{X+1}$ refer to estimates of the abundance of age-group θ at the beginning of year x and of age-group $\theta + 1$ at the beginning of year $x + 1$, respectively, and we have to deal with coefficients for one year only. Although this method is simpler to apply, because the second logarithmic term of (14.86) is no longer needed, its usefulness would depend on the consistency with which any seasonal variation in abundance estimates is repeated from year to year—a complication which is largely avoided by working with estimates of annual mean abundance.

14.3.2 *Application of the methods*

14.3.2.1 *Subtraction of the marking estimate of F from the total mortality coefficient to give M*

The analysis of the post-war plaice marking data given in §14.1.3 was not sufficient to distinguish the 'true' natural mortality rate from the large 'other-loss' rate X, but we were able to obtain a provisional estimate of c. It is therefore possible to obtain estimates of the effective overall fishing mortalities that were generated in the Southern North Sea plaice population by the English steam and motor trawler fleet in 1946 and 1947, and to compare these with the corresponding data for total mortality.

In order to compute $\bar{f}$ from (10.30) we need to know the annual catch in numbers of plaice and the fishing time in each sub-area. English commercial statistics give the annual yield in weight and fishing time in each statistical rectangle, so that we have taken the latter as the unit sub-area. To convert yield in weight to yield in numbers we have used market measurements of plaice, but in 1946 these were obtained from only about two-thirds of the rectangles from which plaice were landed, and these tended to include the more highly fished areas. The first requirement is therefore to use the data of the sampled rectangles, for which both catch in weight and in numbers are known, to see whether any appreciable error would be introduced by computing $\bar{f}$ for the whole area from catch in weight instead of catch in numbers.

For the sampled rectangles therefore, using (10.30) and catch in numbers, we obtained a value of

$$\bar{f} = 19{,}000 \text{ hrs. fishing per rectangle}$$

Now, the average size of a statistical rectangle in the area concerned is 1,086 sq. miles, and the average gross tonnage of vessels in the fleet was 171, so that the above value of $\bar{f}$ in our standard units of fishing intensity becomes*

$$\bar{f} = \frac{19{,}000 \times 171}{1{,}086 \times 1{,}000} = 3.0 \text{ S/T ton-hrs./sq. mile/year} \times 10^{-3}$$

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*Conversion to standard units in this way is, strictly speaking, permissible only if there is no tendency for certain rectangles to be fished consistently by vessels whose average tonnage differs appreciably from that of the fleet as a whole, and if the number of hours fished during a year by a vessel is not a function of its tonnage. In the present case detailed ton-hour statistics were not readily available, but it was found that the above requirements were met to an extent sufficient for the simple conversion to be satisfactory.

Hence our best estimate of the effective overall fishing mortality coefficient resulting from the activity of British steam trawlers in the sampled rectangles in 1946 is given as

$$\bar{F} = c\bar{f} = 0.25 \times 3.0 = 0.75$$

Repeating this calculation using data of catch in weight gave a value of $\bar{f}$, and hence of $\bar{F}$, differing from the above by 1% only, owing to the fact that there was hardly any tendency for the number-density in each rectangle to be correlated with the mean size of fish in it. From this we may conclude that no significant error is likely to be introduced by using catch in weight instead of numbers when computing $\bar{f}$ for the whole area.

For all those rectangles, 75 in number, from which plaice were landed in 1946 by British steam trawlers, using catch in weight, we found a value of

$$\bar{f} = 2.0 \text{ S/T ton-hrs./sq. mile/year} \times 10^{-3}$$

Hence our best estimate of the effective overall fishing mortality coefficient for plaice caused by the British steam trawler fleet in 1946 is

$$\bar{F} = 2.0 \times 0.25 = 0.50$$

The same procedure was followed for motor trawlers, except that conversion to standard units of fishing intensity included multiplying by the factor 1.4 determined in §12.3, to adjust the fishing power of motor and steam trawlers of a given tonnage. In this way we obtained the estimate

$$\bar{F} = 0.04$$

for motor trawlers. The fishing mortality coefficient due to English steam and motor trawlers would therefore appear to have been between 0.5 and 0.6. The complete data for 1947 were not available at the time these computations were made, but the value of F in that year is not likely to have been more than about 10% greater than in 1946.

The plaice age-composition data for 1946 and 1947 indicated that the total mortality coefficient for that period was probably between 1.0 and 1.3 (see Holt, 1949b), so that a mortality of between 0.5 and 0.8 remains unaccounted for.* The available commercial statistics of most other European countries fishing the North Sea plaice are not sufficient to carry out a detailed assessment of the contribution of their fleets to the total fishing mortality rate in the above way, but some indication of it can be gained from the fact that British landings of plaice from the North Sea in 1946 were about one-third of the total (Bulletin Statistique, 1950). If the value of $\bar{F}$ due to British fishing estimated above is raised by the ratio of British to total catch it gives an estimate of total $\bar{F}$ of about 1.5, which is greater than the observed total mortality coefficient. However, not all of the total catch of plaice was taken from the area fished by British vessels in 1946, and raising in this way certainly overestimates the total $\bar{F}$; raising the value of $\bar{F}$ due to British fishing by a factor of two rather than three is probably more correct, which gives a total $\bar{F}$ of the same order of magnitude as the observed total mortality coefficient. While we are unable to make here a more accurate comparison between fishing mortality and total mortality, it is clear that there is no large difference between the two that could be ascribed to natural mortality. At this stage we can therefore say that the natural mortality coefficient in plaice is hardly likely to be greater than 0.2 and is probably smaller.

14.3.2.2 *Simultaneous estimation of F and M from age-composition and fishing intensity data*

We may now consider the methods of §14.3.1, which make use of data of age-composition and fishing intensity over a period of years. Tables 13.1 and 13.2 give the published age-composition data for plaice and haddock for periods of nine and fifteen years respectively, but difficulties arise when an attempt is made to estimate the corresponding fishing intensities on each species. Thus the statistical tables published by the Ministry of Agriculture, Fisheries and Food give the total fishing time by English trawlers for each region of the North Sea, and Raitt (1939) gives comparable data for Scottish vessels; but on each species, and particularly on plaice, there was considerable foreign fishing which we were unable to assess directly. In such circumstances the only possible procedure was to compute indices of total effort by raising the British effort according to the ratio of the British catch to the total catch of the species in question. In assessing the British effort on plaice and haddock some correction could be made for the relative fishing powers of the main types of vessels concerned, and of the introduction of the Vigneron-Dahl gear in the haddock fishery. It was not possible to reduce effort to standard ton-hour units nor to convert it to effective overall intensity.

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*We have not assessed the fishing mortality caused by English seiners, but these were few in number in the years in question, and could have contributed only a very small proportion of the residual mortality.

The detailed computation of European fishing effort on each species is given in Appendix IV and summarised in columns C and E of Table 14.15 together with the corresponding total mortality coefficients (entered against the first year of each pair of years) in columns B and D, these being taken from columns Y of Tables 13.3 and 13.4. Inspection of Table 14.15 shows at once that the relative variation of the fishing effort indices is much smaller than that of the mortality coefficients, and also that such variation as does exist in the former is not obviously correlated with that of the latter. In fact, fitting regressions showed that the slopes (*c*), though positive as would be expected, were not significant; neither did the intersects differ significantly from zero. The method cannot therefore be used to obtain reliable estimates of natural mortality from the pre-war data in either species, but it is instructive to consider briefly why this should be so.

As explained above, the lack of detailed commercial statistics makes it necessary to use estimates of fishing effort instead of intensity. We have no reason to believe, however, that year-to-year changes in the distribution of the effort would have been sufficient to make variation of the effective overall intensity very much greater than that of the effort indices given in Table 14.15. Hence the variation in the mortality coefficients must be ascribed primarily to annual variations in the natural mortality coefficient and to sampling error of the age-composition data of Tables 13.1 and 13.2 from which the total mortality coefficients are obtained. If the former were the only cause of variation, the average value of M in both species must be not less than 0.5; but in the plaice at least we have shown in the previous section that fishing is the major component of the total mortality, and in §14.3.2.3 shall obtain a fairly reliable indication from other data that the average natural mortality coefficient is unlikely to be greater than 0.1. These findings lead to the conclusion that the greater part of the variation of the mortality coefficients of Table 14.15 must be due to sampling error, which is borne out by evidence of another kind to be discussed in §15.2.2.

This attempt to separate fishing and natural mortality in plaice and haddock by the methods of §14.3.1 therefore fails because the sampling error of the total mortality coefficients is too large relative to the range of change of fishing intensity. The latter is indeed so small in both species that a large, and possibly impracticable, increase in sampling effort would have been needed to distinguish the effect of the changes in fishing intensity on the mortality estimates. More usually, however, the expected range of year-to-year variation in fishing intensity can provide a useful guide to the amount of sampling required, since the accuracy of the mortality coefficient estimates (and hence the amount of sampling) needed to obtain estimates of c and M with a given precision varies inversely with the range of change of fishing intensity.

To give a better demonstration of the method we shall discuss three examples of its application to other cases where the above requirements are met to a greater extent than in the plaice and haddock data considered above, the first two being the Fraser river sockeye salmon (*Oncorhynchus nerka*) and the Lake Trout (*Cristivomer namayensh*) of Lake Opeongo, Ontario.

Rounsefell (1949, Table 2) gives mortality data for the Fraser sockeye which is unique in that it extends over a period of fifty-two years during which time the fishing effort as measured by the number of gillnet units of effort given by Rounsefell and Kelez (1938, Table 31) varied over a roughly four-fold range. These salmon data are interesting in the present connection because the exploited population consists almost entirely of a single age-group and is renewed each year; consequently the mortality estimates are obtained from estimates of the total run and subsequent escapement for each year, and we do not require the second logarithmic term of (14.86). Since we are now dealing with a river fishery there is the possibility that the units of gear may not be operating interactively, but as we showed in §8.3.1, it is permissible to regard fishing as interactive if there is a linear regression relating instantaneous total mortality coefficient to fishing effort, that is, if (14.94) gives an adequate representation of the data.

In Table 14.16 we give therefore mortality coefficients and indices of effort obtained from the above-mentioned sources, and in Fig. 14.9 these are plotted and the regression shown. The data are represented well by a straight line—from which we may conclude that the fishery is interactive—and the regression is clearly significant, the intersect being 0.648 and the slope 0.311. The mortality coefficients given in Table 14.16, and hence also the intersect of Fig. 14.9, refer to a fishing season of approximately three months duration, so that they need to be multiplied by four to compare them with the annual coefficients obtained from non-seasonal fisheries. Thus the above intersect is equivalent to an annual coefficient of 2.59, which is large in comparison with even the total mortality coefficients we have obtained previously. It should be noted, however, that the gillnet units of effort to which we are relating the observed mortality do not represent the whole of the fishing to which fish are exposed during the course of a season, so the intersect consists of the mean coefficient due to this residual fishing during the period as well as true natural mortality. This fact does not influence the validity of the slope of the regression, the value of which shows that each unit of gillnet effort generates a mortality coefficient in annual units of about 0.0012.

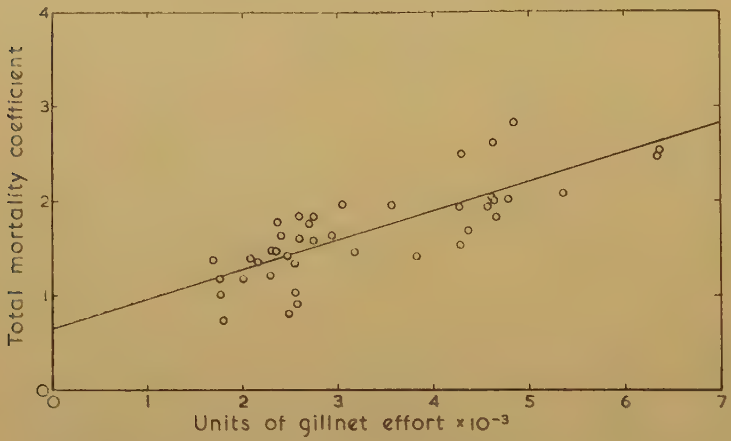

FIG. 14.9
TOTAL MORTALITY AND EFFORT IN FRASER RIVER SALMON

[Plot of total mortality coefficient against corresponding fishing effort (gill-net units) to show linear trend expected from theory; from Table 14.16.]

Turning now to the example based on the Lake Trout, Fry (1949, Table 5) gives age-composition data in the form of catch in numbers per unit effort covering a period of eleven years. In Table 1 of the same paper Fry gives the corresponding fishing efforts; these cover a nearly four-fold range of change and show at first a downward trend followed later by an upward trend. These characteristics have an interesting effect on the use of the methods of §14.3.1 which is the main purpose of giving this example. The fishery is seasonal, but it is sufficient for the present purpose to compute mortality coefficients in units of a year in the same way as we have done in §13.2 for plaice and haddock. For this purpose we have used age-groups VIII and IX, and the resulting total mortality coefficients together with the corresponding efforts are given in columns B and C of Table 14.17.

We may now apply (14.86) to these data, proceeding by the iterative method described in §14.3.1. Three successive estimates of M and c were obtained, and these are tabulated in Table 14.18 together with the corresponding sum of squares of residuals for each regression (U). The third estimates, particularly of M, differ appreciably from the first, and the error in M due to ignoring the second logarithmic term of (14.86) would amount to more than 50% (overestimate). The first value of c is similarly a 20% underestimate of the final value. Also, the process of iteration results in an appreciable decrease in the sums of squares of the residuals U, indicating that the final mortality estimates are better represented by a straight line than are the first.

The above relationships are shown in Fig. 14.10 where the mortality coefficients are plotted against the fishing effort in the first year of each pair. The hollow circles and the dotted line refer to the uncorrected mortality estimates of column B of Table 14.17 and the first regression line respectively; the solid circles and the full line are the final estimates. It will be seen that there is a tendency for the higher mortality estimates to be increased by the iterative process and for the lower ones to be decreased, which has the effect of rotating the regression lines. It is worth noting that although the scatter of the data is such that the intersects do not differ significantly from zero, the error in the estimate of M which would result from ignoring the second logarithmic term would remain as large, however accurate the mortality estimates might be. This point can be seen by considering for a moment the second term itself, which is

$$\log \left\{ \frac{(cf_X + M)\,(1 - e^{-(cf_{X+1} + M)})}{(cf_{X+1} + M)\,(1 - e^{-(cf_X + M)})} \right\}$$

This expression contains no reference to the mortality data but only to the fishing effort, and its magnitude depends on the extent to which the quantity

$$\frac{cf_X + M}{cf_{X+1} + M}$$

differs from unity. This depends not only on the ratio f_X/f_{X+1}, i.e. on the extent to which the fishing effort changes from one year to the next, but also on the magnitude of M. The sign of the whole term depends on whether the fishing effort is increasing or decreasing, being negative when $f_X < f_{X+1}$ and positive when $f_X > f_{X+1}$. In the case of Fry's data the rotation of the regression lines is due to the particular form of the trend in fishing effort.

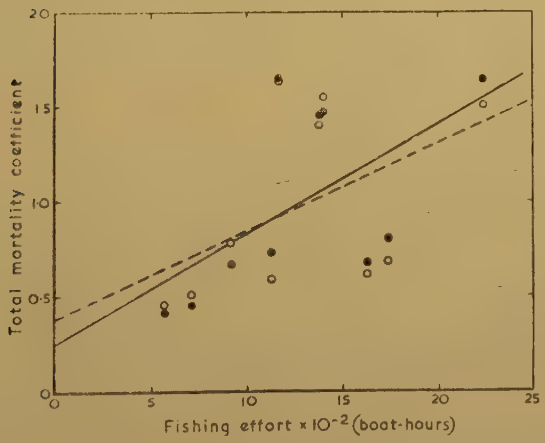

FIG. 14.10 TOTAL MORTALITY AND EFFORT IN LAKE OPEONGO TROUT

[Plot of total mortality coefficient against corresponding fishing effort (boat-hours); from Table 14.17. The two sets of points and associated regressions show the effect of applying the log-correction term of (14.86). ○ and – – – = first estimates, ● and —— = final estimates.]

To sum up, therefore, this example serves to show the circumstances in which the second logarithmic term of (14.86) may be important. Its value will increase as the year-to-year changes in fishing effort increase, the practical importance of this being that it is just when the changes in effort are large that the method is likely to give the best results. Moreover, the presence of a trend in fishing effort may exaggerate the effect of the term on estimates of M and c. Finally, for given changes in fishing effort, its magnitude increases as M decreases, so that the error in M which results from ignoring it will be particularly pronounced when M is small.

For our final example of the methods of §14.3.1 we take the age-composition and fishing effort data for the California Sardine (*Sardinops caerula*) published by Silliman (1943), which is of interest in that the fishery had been stabilised under the influence of two very different levels of fishing effort. This enables us to apply (14.89) to obtain a direct estimate of M. Silliman (ibid, p. 4) gives the total mortality coefficients for the two periods in base 10 logarithms as 0.225 and 0.700 respectively, and converting to natural logarithms we have

$$(F + M)_A = 0.518$$

$$\text{and } (F + M)_B = 1.612$$

which can be substituted in place of the two logarithmic terms of (14.89). Silliman does not give the actual fishing effort in either period but states that it was approximately four times greater in the second period than in the first. In our terminology we can therefore put $f_B = 4f_A$ and from (14.89) we have

$$M = \frac{1}{3}(4 \times 0.518 - 1.612) = 0.153$$

Silliman determined from the same data the "seasonal" natural mortality rate n, as defined by Ricker (1940), which is related to the instantaneous coefficient M by the equation

$$n = 1 - e^{-M}$$

and by trial methods showed that n was a little greater than 0.13333. The value of M obtained above is equivalent to a value of $n = 0.142$.

To conclude this section we would wish to emphasize that the above examples have been presented here solely to illustrate certain aspects of the application of the methods of §14.3.1 which could not be shown with the plaice and haddock data. In each case there are complications which would need to be taken into account in a more thorough investigation; for example, all the above fisheries are seasonal,* the escapement figures given by Rounsefell are not independent of those of the total run but were obtained by subtracting the total catch from the latter, and the gear used in the Lake Trout fishery described by Fry was rod and line for which it is not necessarily correct to represent fishing mortality by means of a simple exponential coefficient. Despite these qualifications, we feel that these examples are of value in showing the application of what may prove to be a useful technique for the analysis of mortality rates in fish populations.†

14.3.2.3 *Direct estimation of M for plaice*

A special case of the above method arises when F has the value zero for a certain period. An approximation to this condition has been found in the plaice by making use of the fact that during the 1939-45 war there was only a small amount of fishing in the Southern Bight, so that the total mortality rate during this period is likely to have been generated mainly by 'natural' death.

The year-classes fully represented in the samples taken at Lowestoft and Grimsby during the last pre-war sampling year (June 1938-April 1939) and yet still present in the samples taken during the first post-war sampling year (December 1945-October 1946) are those of 1931, 1932, 1933 and 1934. In column A of Table 14.19 we give the pre-war estimates of their abundance and in column B the post-war estimates for the corresponding months, the number of fish in the latter samples being given in column C. From the data of columns A and B we can obtain direct estimates of the total mortality between the respective sampling dates as exponential coefficients, and these are given in column D.

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*This fact does not, however, affect the validity of the application of (14.94) to the salmon data.

†C. C. Taylor (unpubl. M.S., 1956) has recently applied this method to the haddock stock of the North-West Atlantic.

There is evidence that there was very little fishing in the Southern North Sea between about January 1940 and December 1945 (Margetts and Holt, 1948), that is, for a period of about six years. We have therefore estimated the total mortality from each pre-war sampling date until January 1940 by taking the appropriate fraction of the total annual mortality rate as obtained from samples taken during corresponding months of the two preceding years. These are shown in column E. A similar procedure for the periods between December 1945 and the post-war sampling dates gives the mortality estimates of column F. The mortality between January 1940 and December 1945 is now obtained by subtracting the sums of columns E and F from the total mortality estimates of column D, the results being given in column G. Finally, we convert these to estimates of the mean annual mortality coefficient during the war period by dividing by six (column H).

Having in mind the small number of fish in the post-war samples the mortality estimates of column H are reasonably consistent. They have a mean value of 0.08 and a mean weighted by the logarithms of the numbers of fish in column C of 0.06; the latter is probably the better estimate if only because taking logarithms eliminates those estimates which depend upon a single fish in the post-war samples. In attempting to obtain a specific value of M from these estimates, however, it must be borne in mind that we have not taken account of the fact that in several cases there were no fish present in certain age-groups of the post-war samples; there were none in any of the relevant age-groups in the samples taken at Grimsby in September 1946, for example. The effect of this is to cause any mean value obtained from column H to be something of an underestimate, but this will tend to be counteracted by the fact that a small amount of fishing probably did take place during the war, of which we have taken no account. Bearing these points in mind it would seem that a value of

$$M = 0.1$$

as an average over the exploited phase of the plaice is a reasonable approximation to the true figure, and we shall use this in subsequent calculations of this paper.

14.3.2.4 *Approximate estimation of M for haddock*

We cannot analyse the plaice data by methods which make use of a knowledge of the relative change in fishing intensity on age-groups within the selection or recruitment ranges, because the data refer to the catch, not the population. The haddock data of Table 13.2, on the other hand, were obtained by sampling the population with the research vessel EXPLORER. The gear used was a normal trawl fitted with a shrimp netting cover, and was kept the same throughout the period. Raitt claimed that this gear gave representative sampling of all fish from the largest to the smallest on each ground, so we shall assume for the moment that the age-composition data of Table 13.2, and hence the estimates of total mortality given in Table 13.4, refer to the 'true' abundance of fish.

We have already noted in §13.2 that only the I-II group coefficient differs appreciably from those of higher age-groups. For the first eleven years of the series the former fluctuates about a mean value of 0.194, but in the last six years it reaches values which approximate to that of the average mortality for the whole of the rest of the population, including in particular the II-III age-group mortality. Raitt showed that in these latter years there was a considerable increase in the average weight of the lower age-groups, which undoubtedly resulted in their becoming liable to capture at a lower age, and would seem a likely cause of the increased I-II age-group mortality during the later years.

We have no accurate knowledge of the shape of the selection ogive of the cod-end mesh which caused the observed age structure of the haddock population during the earlier years, and there is also the possible complication of selection through other parts of the trawl. Nevertheless, some idea of the change of F with age through selection for age-groups I and II can be deduced from the analysis of mesh selection in haddock given in §14.2.2, and from this consideration alone the value 0.19 quoted above should represent the sum of the natural mortality and about one-quarter of the full fishing mortality coefficients. Since we estimated, in §13.2, the mean total mortality coefficient for the higher age-groups to be between 1.1 and 1.2, this gives a value for M of about -0.1. Being negative, this is inadmissible, and although the anomaly could have arisen through sampling errors, it is more likely that data for the abundance of I-group fish are underestimates of the true population frequency of this group. This phenomenon would arise if there had been any escape of fish from that part of the trawl used by the EXPLORER which was not covered by shrimp netting, if there is any tendency for the younger fish to be geographically segregated, or if they are not truly demersal.*

In the absence of further evidence we shall therefore take 0.19 (rounded to 0.2) as our working value in this paper for the natural mortality coefficient of the haddock. From the above considerations it would seem that this figure may be an overestimate, but it will become clear in Part IV that when applying theoretical models to practical fishery problems, the effect of different values of M is such as to make it better to use a value which, if anything, is too high rather than too low. Taking $M = 0.2$ gives an estimate of the mean pre-war fishing mortality coefficient of haddock of 1.0 (see §13.2).

SECTION 15: RECRUITMENT AND EGG-PRODUCTION

We shall discuss the determination of recruitment parameters in two stages, dealing first with recruitment as a function of age (§15.1), and secondly with the estimation of the numbers of fish recruited each year and the relationship between them and the abundance and structure of the mature population from which they originated (§15.2).

15.1 RECRUITMENT AS A FUNCTION OF AGE—THE DETERMINATION OF t_p

The main factor which decides whether recruitment occurs relatively early or late in the life of a fish is whether the nursery grounds are within the main exploited area. If they are, it is possible for recruitment to occur very early; it may, in fact, coincide with the change from a pelagic larval phase to a demersal habit. On the other hand there may often be peculiarities in the behaviour of young fish which make them less liable than older fish to encounters with fishing gear, even though they may have become demersal, and this will have the effect of increasing the age at which recruitment to the true exploited phase occurs. In those cases where the nursery grounds are outside the main fished area, recruitment will usually be the result of the migration of fish from the one area to the other, and a study of it will need to take some account of the way in which this migration occurs and the causes underlying it.

15.1.1 *Haddock*

The authors are not competent to make any detailed statements concerning recruitment in the North Sea haddock, but it is clear from the research on the life-history of this species (e.g. H. Thompson, 1929) that in a general sense it conforms to the first type mentioned above in that the nursery grounds of this species are not separate from the area inhabited by the adults. As was mentioned in §14.3.2.4, the evidence is that while relatively few O-group fish are demersal, the majority of I-group fish have adopted this habit. This suggests that the change from a pelagic to a demersal existence occurs at about the end of the first year of life. For the purposes of calculations to be given in Part IV we shall take t_p to be 1 year in the haddock, and regard fish of this age as effectively below the selection range of the gear in use during the period covered by the data of Table 14.2.

15.1.2 *Plaice—the use of research vessel sample data*

The main nursery grounds of the North Sea plaice are on the Dutch, German and Danish coasts. Recruitment is by migration to the deep-water fishing grounds of the

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*Mr. B. B. Parrish has informed us that there is definite evidence that the O — group are not wholly demersal, and that the same may be true to a much less extent of I — group fish.

Central and Southern North Sea, and in addition to finding the average age at which this occurs, it is desirable to investigate more fully the mechanism of the migration itself, since in §9.2 for example, when considering the effects of a change in the growth rate of the pre-recruit phase, we found it necessary to distinguish between the possibilities of either age or weight being the governing factor.

For determining t_p, the most direct information available about the plaice is that obtained from market samples. As discussed in more detail in §15.1.3, a limitation of these data is that some rejection of the smallest fish occurred, so that the estimate of t_p derived in this way is likely to be a little higher than the true value. In an attempt to eliminate this bias we were led to examine another type of data, namely the results obtained by research vessel sampling of the Leman-Haaks line, a series of stations extending from the Dutch coast to the centre of the North Sea. These were found to be rather less reliable than market samples for the purpose of estimating t_p (though for different reasons), but provided some valuable information concerning the mechanism of the migration and the validity of the concept of random diffusion which was postulated in §§10.2 and 14.1.3.3 to represent the movement of fish. It is convenient to begin by presenting the results of the analysis of the Leman-Haaks data.

15.1.2.1 *Analysis of dispersion of plaice from the nursery grounds to the main exploited area, using the Leman-Haaks data*

Sampling at the Leman-Haaks line of stations was initiated in 1906 as a means of investigating the early stages of the life-history of the plaice, and the average positions of stations are shown in Fig. 15.1. The line of stations was worked again in 1920, and in the years 1922-30, the data for all years being summarised by Borley and Thursby-Pelham (1925, Tables 25-29), Thursby-Pelham (1928, Table 21) and Thursby-Pelham (1932, App. B). In the following we omit the data for three of these years; for 1920 because no cover-net was used, and for 1929 and 1930 because the spacing of stations makes the data difficult to combine with those for previous years.

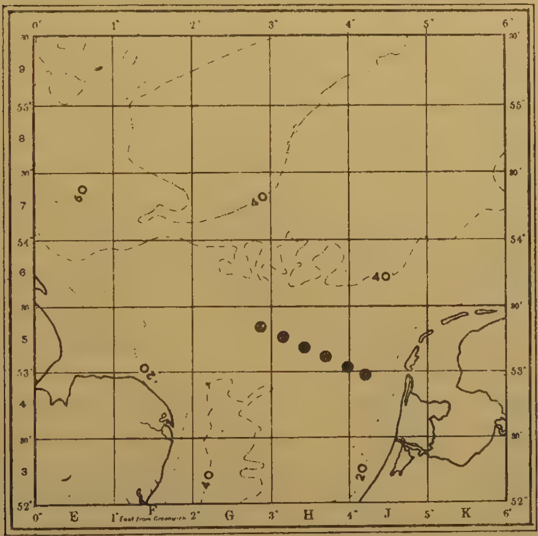

FIG. 15.1
LEMAN-HAAKS LINE OF STATIONS

[The solid circles show the approximate positions of stations at which estimates of density of plaice were obtained. Depth contours in metres.]

The data refer to catches of certain age-groups per hour fishing at each station, and inspection of the Tables cited above shows that there is enormous variation, some of which is undoubtedly due to true differences in abundance of the various year-classes in question. By combining all the data and obtaining the mean density of each age-group at each station for all years except the three mentioned above, it is possible to obtain more consistent and comparable figures. These are given in columns A to E of Table 15.1, together with the mean distance (in miles) of the central position of the haul from the Dutch coast, and they are plotted in Fig. 15.2.1. Although there is a general tendency for the density of each age-group to decrease with increasing distance from the coast, it will be seen that the density of age-groups III, IV and V+* rises sharply at about 35 miles and falls again at about 55 miles distance. Closer inspection shows the existence of a similar though less marked characteristic in the II-group distribution.

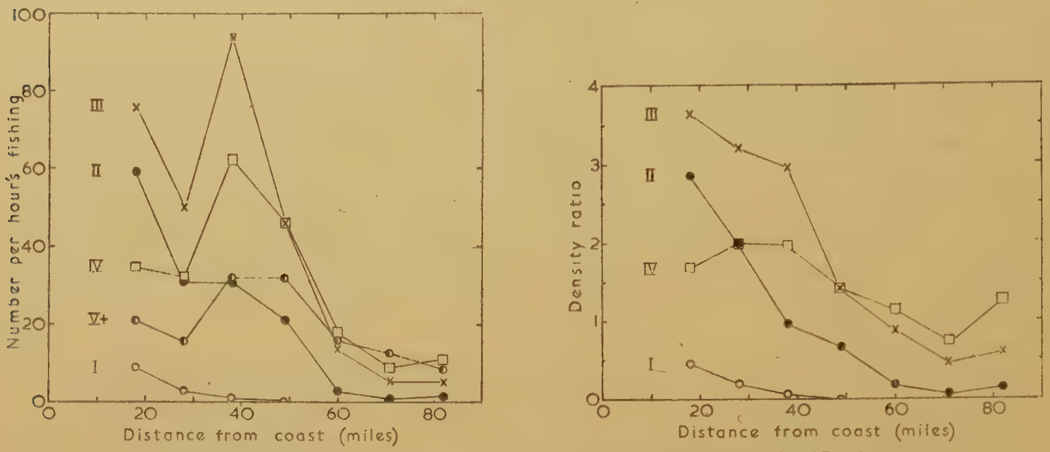

FIG. 15.2.1 FIG. 15.2.2

FIGS. 15.2 DISTRIBUTION OF PLAICE ALONG THE LEMAN-HAAKS LINE; FROM TABLE 15.1

Fig. 15.2.1 Density (catch per hour fishing) of certain age-groups plotted against distance from coast.
Fig. 15.2.2 Ratios of density of age-groups I-IV to density of age-groups V and above, plotted against distance from coast.

Now if we were to suppose that the pattern of migration is such that each age-group moves away from the coast *en masse*, then we should expect to find that the greatest density would occur at about the centre of the distribution of each, so that the distributions would be unimodal. At first sight it might therefore appear that the peaks of the curves of Fig. 15.2.1 indicate the centres of the distribution of the age-groups concerned, but there are two reasons for believing that this is not the case. The first is that the peaks are almost coincident, whereas on the above hypothesis their distance from the coast should increase with age; the second is that the density of these age-groups rises sharply at the innermost station. A more probable explanation would therefore seem to be that the peaks of the distributions indicate an aggregation due to some local factor affecting all age-groups, such as a high concentration of food organisms, rather than a fundamental property of the off-shore migration pattern. Certainly, depth can virtually be ruled out as a factor influencing the distributions, since the average depths at the stations concerned, including the innermost, do not differ by more than a fathom.It is even possible that the increased density may be apparent only, since the effect could be caused by the trawl operating more efficiently at the stations in question than at the remainder.

In these circumstances it would seem that a better understanding of the off-shore movement is to be obtained by calculating the distribution of each age-group relative to that of the V + fish, and these ratios are given in columns F to J of Table 15.1. When they are plotted, as in Fig. 15.2.2, it is found that in most cases the points fall on smooth descending curves with no suggestion of a mode. The fact that by taking ratios we have been able to eliminate the peaks of the original distributions without 'over-compensating', gives substantial support to our previous conclusion that they are due to some local factor affecting all age-groups more or less equally. It may well be, of course, that the distribution of each age-group has a mode before the actual shore line is reached, but this does not seem to be an important feature of the migration. The impression gained from Fig. 15.2.2 is that the off-shore movement consists of a gradual dispersion away from a coastal zone that is extremely narrow relative to the whole area over which the fish will eventually spread The shapes of the curves of Fig. 15.2.2 are, in fact, similar to those which would be found if the individual fish were moving randomly in the sense postulated in §10.2, and from this evidence the off-shore movement of plaice would seem better described as a process analogous to *diffusion*, rather than as an oriented migration with each year-class moving away from the coast as a whole. In what follows, this conclusion, which is similar to that reached by Borley (1916) about the movement of marked plaice liberated on the Dogger Bank, is tested further.

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*Age-groups V and above are not considered separately in the original data, and the symbol V+ denotes the sum of the catches of all these age-groups.

In §10.2.1 we introduced the concept of random diffusion by giving the general partial differential equation (10.2) defining the probability density at a point x , y at time t, viz:

$$\frac{\partial C}{\partial t} = \frac{D}{4}\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right)$$

It will be remembered that D of this equation is the dispersion coefficient and can be regarded as proportional to the mean velocity of the fish. In §10.2 we used, instead of D (the instantaneous coefficient of the rate of change of density with respect to time and distance), its finite-difference equivalent T, so that the treatment was more suitable for use with the kind of data obtainable from commercial statistics of catch and effort. In the present case we have abundant data referring to accurately known times and positions, so that, as in the 'point-release' marking technique suggested in §14.1.2.4.3, it is more convenient to use the instantaneous coefficient D.

Studies such as those of Heincke (1905) and Redeke (1905) on the distribution of larval plaice along the eastern shores of the North Sea show that the Leman-Haaks line of stations was not near the northern or southern limits of the distribution. In order to set up a theoretical model representing the dispersion of plaice along the Leman-Haaks line we can therefore suppose that changes in density occur only in a direction at right angles to the coast; thus we need deal only with models of dispersion in one dimension. A further condition is that dispersion can occur only away from the coast, so that (10.2) can be written as

$$\frac{\partial C}{\partial t} = \frac{D}{4}\frac{\partial^2 C}{\partial x^2} \quad \cdots \quad (15.1)$$

This equation can be solved by expanding to give a Fourier series, provided the particular boundary conditions are specified. Since we are concerned primarily with the process of dispersion while the majority of the fish are still on the eastern side of the North Sea, we can consider the area as unbounded to the west, i.e. we can disregard any 'reflection' from the English coast. The solution of (15.1) then becomes

$$C_{x,t} = \frac{C_0 e^{-(x^2/Dt)}}{\sqrt{t}} \quad \cdots \quad (15.2)$$

Now the integration constant, C_0, in our case defines the density of a year-class when at a given age t and before the process of dispersion begins. It is not necessary, however, to suppose that in these circumstances the fish are of zero age and at zero distance from the coast, and we shall postulate that the off-shore dispersion begins when fish are of age t_0 (taking the birthday as April 1st) and that they are then located at a short distance x_0 miles from the coast. Thus (15.2) becomes

$$C_{x,t} = \frac{C_0 e^{-[(x-x_0)^2/D(t-t_0)]}}{\sqrt{(t-t_0)}} \quad \cdots \quad (15.3)$$

The theoretical model represented by (15.3) is illustrated in Fig. 15.3, and it is seen that the situation is analogous to the conduction of heat along a metal bar of infinite length, the source of heat being a thin lamina placed at one end of the bar, and the whole system being surrounded by a perfectly insulating medium—a physical system which has been studied in some detail.

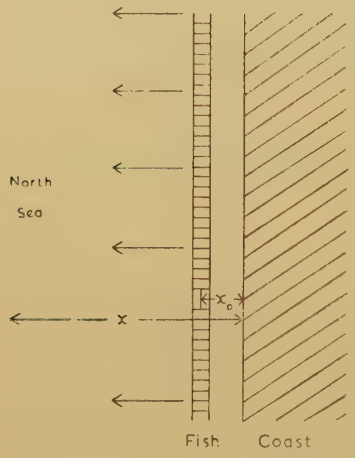

FIG. 15.3 THEORETICAL MODEL OF DISPERSION OF YOUNG PLAICE FROM NURSERY GROUNDS

[Fish are taken to be concentrated initially (at age t_0) in a narrow band at distance x_0 from the shore.]

Before we can proceed to the analysis of the data, there is one further feature which must be incorporated into our model. So far we have been assuming that the total number of fish remains constant, but in practice there will be losses as the result of natural mortality, and also fishing mortality among the older fish. If we denote the instantaneous mortality coefficient by m, and assume for the moment that this is constant, then the original differential equation (15.1) can be restated in the form*

$$\frac{\partial C}{\partial t} = \frac{D}{4}\frac{\partial^2 C}{\partial x^2} - mC \qquad .. \qquad .. \qquad .. \qquad (15.4)$$

having a solution

$$C_{x,t} = \frac{2N_0 e^{-m(t-t_0)-[(x-x_0)^2/D(t-t_0)]}}{\sqrt{\pi D(t-t_0)}} \qquad .. \qquad (15.5)$$

The relationships of this equation can best be seen by using it to deduce an expression for the total number of fish of age t along the whole length of the line at right angles to the coast along which dispersion is being considered. The expression is:

$$N_t = \int_0^\infty C_{x,t}\, d(x-x_0)$$

and substituting from (15.5) gives

$$N_t = \frac{2N_0 e^{-m(t-t_0)}}{\sqrt{\pi D\,(t-t_0)}}\int_0^\infty e^{-[(x-x_0^2)/D(t-t_0)]}\, d(x-x_0) = N_0\, e^{-m(t-t_0)} \qquad .. \qquad (15.6)$$

as required.

Now let us consider the form of the data presented in Table 15.1. In the first place we do not have the true density $C_{x,t}$ but only an index of it, which we denote by $C'_{x,t}$, and write (see §14.1.2.4.3)

$$C_{x,t} = K_{x,t} \cdot C'_{x,t}$$

where $K_{x,t}$ is a coefficient defining the sampling efficiency of the gear with respect to fish at a distance x from the coast and of age t. Thus K may not necessarily be constant for all age-groups owing to the different sampling power and selectivity of the gear for fish of different sizes. We shall, however, suppose that K for a given age-group is constant for all values of x, bearing in mind that if K does in fact vary with x, such variation will probably have been eliminated by taking age-group ratios. In other words, if $K_{x_1 t_1} > K_{x_2 t_1}$ we expect to find that $K_{x_1 t_2} > K_{x_2 t_2}$ in the same proportion, and the fact that smooth distributions were obtained by taking ratios of age-groups supports this assumption. The second complication is that we have converted the original data into relative units by taking the ratio of the density of each age-group to that of all fish five years old and more. Since the majority of the latter will be V-group fish and since it would appear from Fig. 15.2.2 that by the time fish reach this age the process of dispersion is virtually complete, we shall take it that the distribution of the V-group fish would be the same as that of the V+ fish. For the following analysis the data of Table 15.1 referring to V+ fish are regarded as identical with those which would have been obtained for V-group fish alone.[*]

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*This is analogous to equation (11) deduced by Skellam (1951a) to express the combined effect of dispersal and population growth in a Malthusian population in a linear habitat.

The data of Table 15.1 were obtained in the same month (May) of each year, so that denoting by t_θ the actual age of fish of age-group θ on this date, and remembering that K is taken to be constant at all values of x for a given age-group, we can write (15.5) in the form

$$C'_{x,\theta} = \frac{2N_0 e^{-m(t_\theta - t_0) - [(x - x_0)^2/D(t_\theta - t_0)]}}{K_\theta \sqrt{\pi D (t - t_0)}}$$

Taking the density of each age-group as a fraction or multiple of that of the V-group fish, we have

$$\frac{C'_{x,\theta}}{C'_{x,\mathrm{V}}} = \left(\frac{K_\mathrm{V}}{K_\theta} \sqrt{\frac{t_\mathrm{V} - t_0}{t_\theta - t_0}}\right) e^{m(t_\mathrm{V} - t_\theta) - 1/D[(1/t_\theta - t_0) - (1/t_\mathrm{V} - t_0)]\,(x - x_0)^2} \quad .. \quad (15.7)$$

where t_V is the age of fish of age-group V in May, taken to be 5.2 years. The ratio on the left hand side of (15.7) refers directly to the data of cols. F, G, H and J of Table 15.1, and we now need to see whether (15.7) provides an adequate fit to these data, and, if so, to obtain estimates of the parameters D, x_0 and t_0.

The first step is to convert (15.7) to a linear form by taking logarithms, thus:

$$\log\left(\frac{C'_{x,\theta}}{C'_{x,\mathrm{V}}}\right) = \log\left(\frac{K_\mathrm{V}}{K_\theta} \sqrt{\frac{t_\mathrm{V} - t_0}{t_\theta - t_0}}\, e^{m(t_\mathrm{V} - t_\theta)}\right) - \frac{1}{D}\left(\frac{1}{t_\theta - t_0} - \frac{1}{t_\mathrm{V} - t_0}\right)(x - x_0)^2 \quad .. \quad (15.8)$$

If the off-shore migration obeys the laws of random diffusion we should therefore find that the logarithms of the density ratios when plotted against the square of the distance from the origin of dispersion fall on a straight line. We do not yet know the exact position of the latter, i.e. the value of x_0, but if we try putting x_0 = zero we obtain the results shown in Fig. 15.4, which clearly show that the linear relationship predicted by (15.8) gives a satisfactory representation of the data for each age-group in question. Trials with other values of x_0, and calculating the resulting sums of squares of residuals, showed that the best fit is obtained with a value of x_0 slightly greater than zero, i.e. about 2-3 miles; the improvement over that with x_0 = zero was very slight, however, and for this analysis we shall accept this latter value. Nevertheless, it is interesting to find that x_0 may be of the order of a very few miles since it is in accordance with what is known about the distribution of very young plaice; moreover, if the theoretical model we are using were not applicable in this case, we might well have obtained a value of x_0 greatly different from zero—perhaps even negative.

The linear regression coefficients ${}_\theta a_0$ and ${}_\theta a_1$ for each age-group are given in Table 15.2. These were obtained by the method of least squares, with weighting coefficients taken as the square root of the observed density of the age-group appearing in the numerator of each

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[*] This procedure has no effect on the relative distribution of each age-group, but we shall need to return to this question at a later stage when dealing with the determination of mortality.

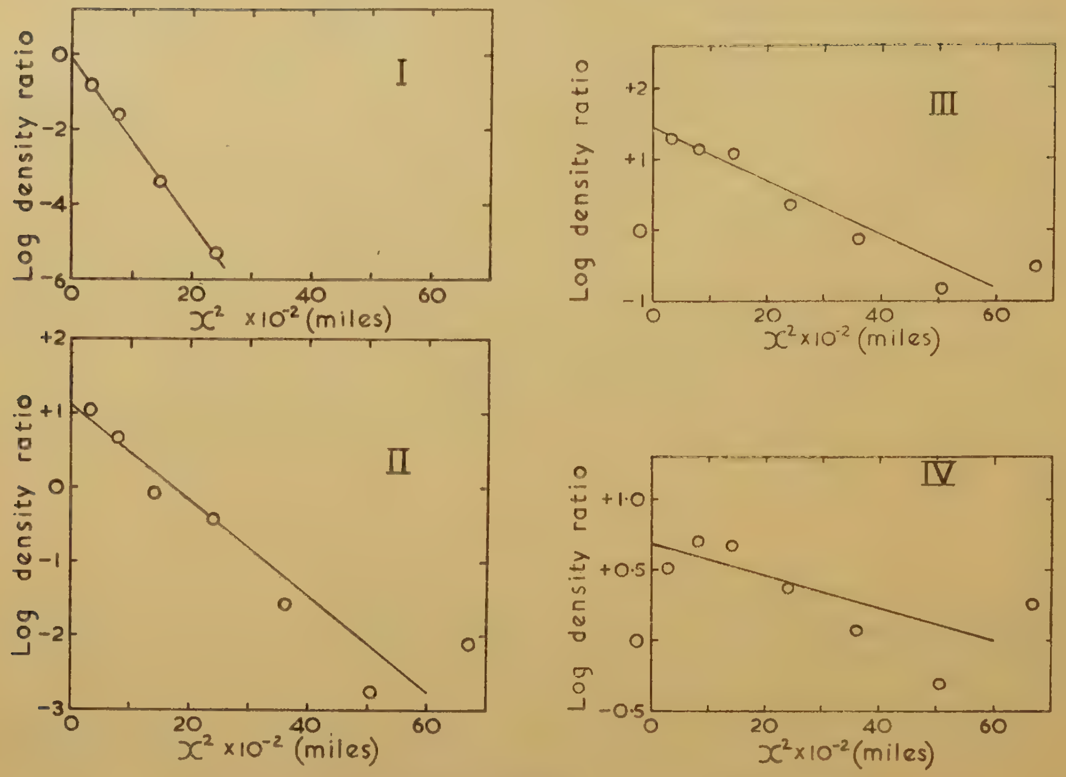

FIG. 15.4 OFF-SHORE DISPERSION OF YOUNG PLAICE

[Logarithms of density ratios (C'_θ/C'_V, see Fig. 15.2.2 and Table 15.1) plotted against square of distance from coast (x^2) for age-groups I to IV, with theoretical regressions predicted by (15.8) and having coefficients given in Table 15.2. The linearity of the trends suggests that the basic pattern of dispersion is random.]

ratio. This was done because of the very great differences in density at the various stations.* Now the ${}_\theta a_1$ coefficients, which are the slopes of the regression lines, are given from (15.8) by the equation

$$ {}_\theta a_1 = \frac{1}{D}\left(\frac{1}{t_\theta - t_0} - \frac{1}{t_V - t_0}\right) \quad \ldots \quad \ldots \quad \ldots \quad (15.9) $$

so that if we choose t_0 correctly we should obtain a proportional relationship between ${}_\theta a_1$ and the expression in brackets, the proportionality coefficient being $1/D$. As with the determination of x_0, we have taken the value of t_0 as that which minimises the sum of squares of residuals, in this case with the restriction that the fitted line must pass through the origin. The graph of (15.9) using $t_0 = 0.5$ is shown in Fig. 15.5, and it is seen that the values of ${}_\theta a_1$ lie close to the fitted straight line passing through the origin with a slope of

$$ \frac{1}{D} = 0.00181 $$

so that $D = 552$ miles^2/year.

Heincke (1905) states that the earliest demersal stages are found between June and August in shallow water close to the shore. The above value of t_0 implies that the young fish begin their off-shore dispersion at the end of September, and is thus in reasonable agreement with Heincke's observations. This being so, the closeness with which the data of Fig. 15.5 are fitted by a straight line can be taken as indicating that the rate of dispersion

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*The accuracy of the denominator, i.e. the density of the V-group fish, also enters into the accuracy of the density ratios, but the V-group density varies much less from one station to the next and can be regarded as being estimated with nearly the same accuracy throughout.

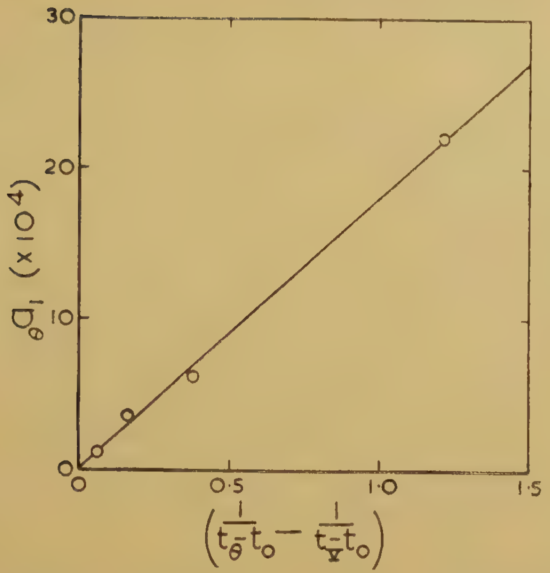

FIG. 15.5 OFF-SHORE DISPERSION OF YOUNG PLAICE

[Slopes of regressions ($_\theta a_1$) shown in Fig. 15.4 plotted against the function of age defined by (15.9), with $t_0 = 0.5$ yrs. The reciprocal of the slope of the line fitted to these data is the dispersion coefficient D, and has the value 552 miles²/year.]

of fish of all the four age-groups in question is similar, despite the fact that the older fish are considerably larger than the younger. This result may seem anomalous at first sight, but D'Arcy Thompson (1948, p. 33) has deduced on theoretical grounds that although the larger of two fish should have a greater *maximum* velocity than the smaller (roughly changing with the square root of their linear dimensions), the net distance travelled over a long period of time by each ought to be similar. It needs to be remembered that most plaice in age-groups I-IV are immature and we might expect to find a difference in rate of dispersion between these and mature fish. The work of Thompson and Herrington (1930) on the Pacific halibut indicates that in this species mature fish disperse more rapidly than immature.

The results of this analysis of the recruitment migration in plaice strongly suggest that the basic mechanism is one of random dispersion, and this conclusion lends valuable support to the validity of the theoretical treatment of §10.2, which is based on the concept of random movement. The fit of the predicted distributions of the density ratios for each age-group is shown in Fig. 15.6, in which the points are the figures of columns F, G, H and J of Table 15.1 and the curves are those given by (15.7) using the values of parameters determined above.

Before proceeding to the question of whether it is possible to determine a value of t_ρ from this analysis, it is of interest to compare the value of D found above with those of the transport coefficient T determined in §14.1.3.3. It is defined in units of miles²/year, so that the time units are the same as those in which T was measured, but an adjustment is needed to make the distance units comparable. Thus if we now regard D as a finite-difference transport coefficient it can be taken as referring to transport of fish out of an area one mile square, and although a precise comparison between transport coefficients relating to areas of different sizes is difficult, an approximate adjustment can be obtained by multiplying by the appropriate perimeter/area ratio (see §10.2.1). Now the estimates of T refer to a statistical rectangle having a perimeter/area ratio of 120/1086; the above value of D can therefore be taken as approximately equivalent to a value of T of

$$\frac{552 \times 120}{4 \times 1086} = 15$$

and this, if anything, is probably an overestimate. In §14.1.3.3 we obtained an estimate of T for rectangle G4 of 7 and a value of 14 for the surrounding five rectangles; but the former value is certainly too low for this comparison since G4 is an area in which fish show a marked tendency to aggregate (see §14.1.3.3) and in which the rate of dispersion is probably

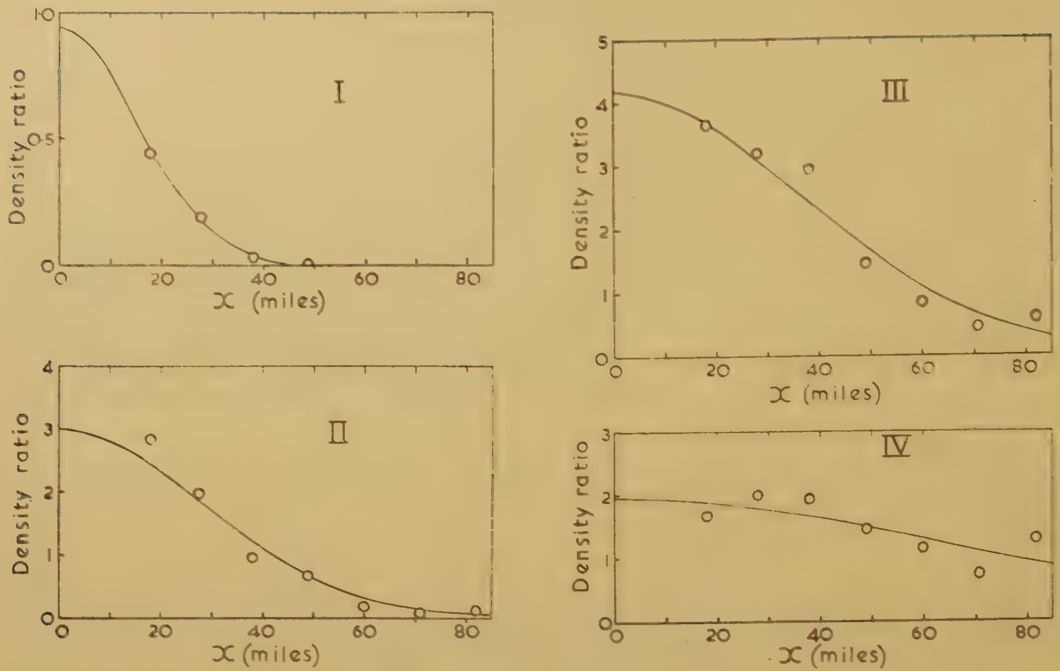

FIG. 15.6 PLAICE DISPERSION

[Density ratios (see Fig. 15.2.2 and Table 15.1) plotted against distance from coast (x) for age-groups I to IV, with distributions predicted on basis of random diffusion (calculated from (15.7)).]

as low as anywhere in the North Sea. Bearing in mind that the present data and those used to arrive at these estimates of T (i.e. from marking experiments) are of entirely different kinds, the agreement is very satisfactory.

In view of the small amount of information which seems to exist relating to dispersion rates in natural populations, it is interesting to compare the dispersion coefficients determined here for plaice with those for the sheep blowfly (Gilmour, Waterhouse and McIntyre, 1946) and certain species of *Drosophila* (Burla *et al.*, 1950) see §10.2.1). These authors do not give actual coefficients, but they can readily be calculated from their data, as follows.

Taking first the sheep blowfly data, the authors give estimates of the Dispersal Index (x) obtained from four experiments (see Table 5, p. 18). This index is defined as the radius in miles of the circle centred on the point of release beyond which half the flies have dispersed after 2½ days from time of release, and the values vary from 0.43 to 2.15 miles. Now we mentioned in §14.1.2.4.3 that if individuals are dispersing randomly their density at distance r from the point of release after time t is proportional to $e^{-r^2/Dt}$, and this enables estimates of the dispersion coefficient D to be calculated from those of the Dispersal Index x. Thus the radius of the circle within which lie half of all flies released, i.e. the value of x, is given from the equation

$$\int_0^x 2\pi r\, e^{-r^2/Dt}\, dr = \frac{1}{2}\int_0^\infty 2\pi r\, e^{-r^2/Dt}\, dr$$

from which

$$e^{-x^2/Dt} = \frac{1}{2}$$

and hence

$$D = \frac{x^2}{0.693t}$$

In the sheep blowfly data, $t = 2.5/365 = 0.0069$ yrs., so that for a Dispersal Index of $x = 0.43$ miles we find

$$D = \frac{0.43^2}{0.693 \times 0.0069} = 39 \text{ miles}^2/\text{year}$$

while a value of $x = 2.15$ miles gives the estimate $D = 967$ miles^2/year. The rate of dispersion found for plaice therefore lies between these two extreme values for sheep blowfly.

Turning now to the *Drosophila* data, Burla *et al.* give estimates of the variance of the distribution of the flies per day after release. For *D. willistoni* this varies between 258 and 828 metres^2/day, and from the above relationships we find that D lies between about 0.07 and 0.2 miles^2/year. These authors also quote estimates obtained by Dobzhansky and Wright (1943, 1947) for *D. pseudoobscura*, which lie between 1500 and 8000 metres^2/day, and are thus equivalent to values of D between about 0.4 and 2.3 miles^2/year. There is therefore a roughly ten-fold difference between the dispersion coefficients for the two species of *Drosophila* under the conditions prevailing during these experiments but all are very much smaller than the coefficients for either plaice or sheep blowfly.

In the above experiments it was found that certain environmental factors, such as wind strength, humidity and temperature, can affect the rate of dispersion; the last of these may also be important in plaice, but we have not investigated this point and it is probable that more extensive data would be required to demonstrate the effect*.

15.1.2.2 *Estimation of* t_ρ

Having analysed the mechanism of the recruitment migration and determined a value for the dispersion coefficient, it remains to see whether the data can provide an estimate of the mean age of recruitment, t_ρ. One method that suggests itself in this case is to determine the value of the mortality coefficient m in successive years of life, since when this takes on the value of the total mortality coefficient in the exploited phase we may presume that all fish of this age-group are fully available to capture and are fully recruited to the exploited area. For this purpose we need to return to the intersects, ${}_\theta a_0$, of the regression lines of Fig. 15.3 which are given in Table 15.2. From (15.8) we find that

$${}_\theta a_0 = \log\left(\frac{K_V}{K_\theta}\sqrt{\frac{t_V - t_0}{t_\theta - t_0}}\right) + m\,(t_V - t_\theta)$$

so that subtracting ${}_{\theta+1}a_0$ from ${}_\theta a_0$ and remembering that $t_{\theta+1} - t_\theta = 1$, we have

$$m_\theta = {}_\theta a_0 - {}_{\theta+1}a_0 + \log\left(\frac{K_\theta}{K_{\theta+1}}\sqrt{\frac{t_\theta - t_0}{t_{\theta+1} - t_0}}\right) \quad \ldots \quad \ldots \quad (15.10)$$

In this way we can determine the mortality coefficient for each year of life without assuming that it remains constant over all the years covered by the data. If we let $K_\theta = K_{\theta+1}$, i.e. if we assume that each age-group is sampled by the gear with equal efficiency, then the right hand side of (15.10) can be computed to give estimates of m between successive ages t_θ and $t_{\theta+1}$, i.e. for each age-group. These are as follows:—

Age-Group	m
I	-1.606
II	-0.556
III	0.591
IV	0.556

---

*Holt (1955) gives an example of the method of examining dispersal data to identify the effects of environmental factors, with special reference to temperature and air currents.

It is clear that it is not permissible to assume that age-groups I and II are sampled with the same efficiency as are age-groups III and IV, since a negative mortality coefficient implies that less fish are present at age t_θ than at age $t_{\theta+1}$ which is absurd. We must therefore consider this point in further detail.

From the analysis of mesh selection for plaice given in §14.2.1 we can be fairly sure that fish of age-groups III and IV are adequately sampled by an ordinary commercial trawl with a 70 mm. cod-end mesh; moreover, the cod-end of the trawl used to sample the Leman-Haaks line of stations was covered with shrimp netting. However, it will be remembered that we have hitherto been treating the data of V + fish as if they referred to V-group fish alone, so that to this extent we have been overestimating the true abundance of V-group fish. From the age-composition data obtained from market samples and given in Table 13.1 we found that fish of five years of age and above were liable to the full mortality rate, of which we obtained the estimate $(F+M) = 0.83$ (see §13.2). If the same applies to the present data we can use (5.3) to estimate what proportion, on the average, of V + fish consists of V-group fish, and this is found to be 0.564. Thus we should multiply the ratio K_{V+}/K_V by 1/0.564 in order to make the IV- and V-group data comparable, and recalculating the mortality coefficient between ages 4.2 and 5.2 years in this way gives

$$m_{IV} = 1.13$$

This figure is in reasonable agreement with the total mortality coefficient found previously, and indicates that fish of age-group IV are fully recruited. The value of m for age-group III is only about half this amount, so that this analysis suggests that t_ρ might be about 3 years.

Little more can be done with the I and II-group data except to find the value of the ratio $K_\theta/K_{\theta+1}$ which when used in (15.10) will give a mortality coefficient of zero in each case, instead of a negative value. This will provide a minimum estimate of the extent to which the gear is incompletely sampling the abundance of these groups relative to that of the older fish. The required values are found in this way to be

$$K_I/K_{II} = 5.0$$

and

$$K_{II}/K_{III} = 1.7$$

indicating that the gear was catching II-group fish not much more than half as efficiently, and I-group fish only about one-ninth as efficiently, as the older fish. This result may have some practical value, as we do not know of any experiments made to determine the sampling efficiency of a commercial trawl with a covered cod-end for plaice between one and three years of age. Although such a gear has been widely used for research vessel sampling it seems that it must be regarded as a very inadequate method for determining a true index of density of plaice of these ages.

It is important to note that although it is not possible to proceed further with this method of estimating t_ρ owing to limitations of the sampling technique, estimates of the parameters x_0, t_0 and D are not thereby invalidated because they were obtained from the *slopes* of the regression lines of Fig. 15.4, values of which do not depend on those of the ratio $K_\theta/K_{\theta+1}$ (see (15.8)). Potentially, the method may be a useful one because samples of the commercial catch are not fully representative of the youngest fish (see §15.1.3), and more frequent sampling along several lines of stations using suitable gear should enable a reasonably accurate estimate of t_ρ to be obtained. Work at present being carried out jointly by the English and Dutch fisheries research staff should meet this requirement.

15.1.2.3 *Further comments on the mechanism of recruitment in plaice*

Although the conclusion that the recruitment migration of plaice is essentially a random dispersion from the coastal belt seems well established, there are certain features of it that are not adequately accounted for by the simple theory we have used, and which deserve further comment.

Perhaps the most important is that if it is assumed that fish older than five years disperse at the same rate as the younger on which the above analysis is based, it leads to the conclusion that detectable numbers of recruits should appear in several age-groups above V. However, this is contrary to the evidence from market samples of the commercial catch (see §15.1.3) which we have every reason to believe are truly representative of fish of age-group V and above. It is clear, therefore, that the simple treatment cannot be extrapolated to older fish, and this might be expected in view of the fact that nearly all five year old plaice are mature and undergo directional migrations to the spawning grounds in the Southern Bight. At the same time, the fact that the nursery grounds contain appreciable numbers of older fish, as can be seen from Fig. 15.2.1, means that interchange of adult fish between the nursery grounds and the main exploited area may be important, in which case it could be taken into account by methods such as those suggested in §10.2.*

Modifications of the simple theory of random dispersion to represent feeding aggregations and directional spawning migrations have been outlined in §§10.2.4 and 10.2.5. The links between these and the off-shore dispersion theory may lie in treating the area into which dispersion occurs as limited, instead of being unlimited as was done in the above analysis. That simplification has little effect on the predicted distributions of the young fish but becomes progressively more important with older fish. With a limited area, the steady state to which the distribution of each year-class tends is that of a finite density over the whole area, thus including the nursery grounds. With an unlimited area the final density is, of course, infinitely low.

Another implication of the theory of random diffusion on which we have based the above analysis is that the expected velocity of each particle (i.e. fish in the present context) should be the same. There may be an instantaneous distribution of velocity, but there should not be a particular particle with a velocity permanently different from the average, and, in fact, the mean distance (not necessarily in a straight line) covered by each particle over a long period of time should be the same. In the case of fish, however, we might expect to find that there are permanent differences in activity among members of a year-class, and this is a modification which in the future may need to be incorporated in the theory as applied to the movements of fish.† Although it would be difficult to detect the presence of a permanent variation in activity from the particular data we have analysed above, it is interesting to find that weight-at-age determinations from the same data as given in Table 15.1 show that the average size of fish of any given age-group increases with distance from the coast. This is shown clearly in the figures presented by Thursby–Pelham (1928, Figs. 5 and 6), in which the average length of III-group fish, for example, ranges from 17 cm. at the innermost station to 23 cm. at the outermost. Now if there is a variation of activity among individuals of a year-class, manifest as a variation either in swimming speed or in the number of 'steps' made per unit time (see §10.2), one consequence will be that the average activity of all those fish which have dispersed beyond any given distance from the coast after a certain time will be greater than that of the remainder. If there is such a variation of activity it therefore follows that the most active fish are also those with the fastest growth. This is not to say that faster growth or larger size is the *cause* of the greater activity; if this were the case we should expect to find that the dispersion coefficient D increased with age, whereas Fig. 15.5 gives no evidence of this.‡ Neither does the fact that it is the largest individuals that have moved farthest from the origin in a given time prove that there is a distribution of activity, since the larger size may simply be the result of the fish in question being the first to reach areas of high food density. To prove the existence of a true variation of activity it would be necessary to measure activity under experimental conditions, or to obtain a more fundamental index such as the rate of oxygen consumption or some other indication of metabolic state, and see whether this tended to be highest among the members of a year-class caught farthest from the coast.

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*From the results of certain trial assessments presented in §18.7 it appears that when a fair proportion of the exploited phase of the population is not fished, departure of the behaviour of the population from that predicted by the simple models of Part I may be appreciable.

†Skellam (1951b) has shown theoretically that when there are permanent differences in activity among individuals the distribution is leptokurtic. We note also that Dobzhansky and Wright (1947) and Burla *et. al.* (1950) found evidence of leptokurtosis in experiments on the dispersion of *Drosophila spp.*, and the latter authors suggest that this might be due to abnormal stimulation of certain flies, or to some flies being weaker than the remainder; in either event the result would be a distribution of activity during the experiments. The problem has also been discussed by Bateman (1950).

‡It is true that we have adjusted the value of t_0 so as to obtain the best fit to a straight line, but we mentioned other evidence indicating that t_0 is not likely to differ greatly from the value we have found.

Leaving aside the question of whether growth and activity are causally related or whether activity is distributed in the way suggested above, we must consider the implications of the fact that the average size of members of a year-class increases with distance from the coast. If we regard recruitment to the exploited area as being the process of crossing the boundary of the latter from the nursery grounds, the youngest recruits of a year-class will be those that have moved farthest from the origin of dispersion and their weight will be above the average weight for the year-class as a whole. Similarly, the recruits whose age is roughly the same as the average age of all recruits will have a size corresponding roughly to the mean size in the whole year-class, while the oldest recruits will be below average size. If the variation of weight-at-age is sufficient it may be that recruits of all ages are about the same average size, and that this is possible in plaice can be seen from Thursby-Pelham's data cited above, where the largest III-group fish are about the same size as the average IV-group fish and as the smallest V-group fish. Thus there will appear to be something like a threshold size for recruitment (see [8.3]) the magnitude of which will depend on the distance between the boundary of the exploited area and the origin of dispersion. Evidence to suggest that such a threshold size exists will be presented in [16.3], but the important point at this stage is to note that this phenomenon and the hypothesis that the mechanism of the recruitment migration is primarily one of random dispersion are not incompatible.

15.1.3 *Plaice—analysis of market sample data*

We now attempt to estimate t_r from the entry of fish to the exploited area, i.e. into the exploited phase, instead of their exodus from the nursery grounds as previously, and we analyse from this standpoint the plaice age-composition data obtained from market samples of the commercial landings. Since we shall be attempting to deduce the age-composition of the exploited phase of the population from samples of the landings, we must first consider the possible effects of gear selectivity and minimum legal size limits on the age-composition of market samples of plaice.

The youngest age-group normally present in market samples is the II-group, but it is clear from Figs. 15.2 that the numbers of I-group fish which are recruited can only be small, so that the question of whether their absence from the catch is due to selection by the gear is unimportant. Now the growth rate studies to be presented in [16.2.1] indicate that the average length of II-group plaice is about 19-20 cm., but those individuals of this age-group that are recruited are those which have moved the greatest distance off-shore, and as we have mentioned above there is evidence to show that the weight of individuals of the age-groups with which we are concerned increases considerably as distance from shore increases. In other words, the average length of those II-group fish which are recruited will be greater than 20 cm.* In [14.2.1] we showed that the mean selection length for plaice by the 70 mm. cod-end used by the British trawler fleet is about 15 cm., and that all fish above about 19 cm. are retained by the gear. These facts indicate that market samples of the commercial catch are unlikely to be influenced by gear selection.

The effect of prohibiting the landing of fish below a certain minimum size is more difficult to assess. A size limit for plaice of 23 cm. was first imposed in 1933, but lapsed from 1939 to 1946, in which latter year a higher limit of 25 cm. was introduced. Nevertheless some rejection at sea took place prior to 1933, and from the data given by Thursby-Pelham (1928) it seems that fish below 21-22 cm. were not usually retained, though unfortunately no age-determinations of rejected fish were made so that accurate adjustment is impossible. A probable consequence of the introduction of a legal size limit was that vessels tended to fish less on those grounds near the nursery areas where small fish were abundant, with the result that the distance of the effective boundary of the exploited area from the coast was increased. This would have caused the value of t_p to increase, so that it does not necessarily follow that greater quantities of fish were rejected at sea after the legal size limit had been imposed than before. Now the age composition data of Table 13.1 were adjusted by Thursby Pelham so as to exclude all fish below 23 cm. from samples taken between April 1st, 1929 and May 31st, 1933 (i.e. during the period prior to introduction of the size limit), but we have had access to the original data in which this adjustment does not appear. Bearing all these points in mind it would seem that at the present time the most satisfactory estimate of t_p for the pre-war period is to be obtained from these original data, since any apparent increase in the value of t_p will tend to be offset by the fact that the introduction in 1933 of a legal size limit probably did cause a *real* **increase in t_p.**

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*The average length of II-group plaice in market samples is 25.5 cm., though this figure is probably an overestimate of the true average length of recruited II-group fish owing to rejection at sea of fish below the minimum size limit.

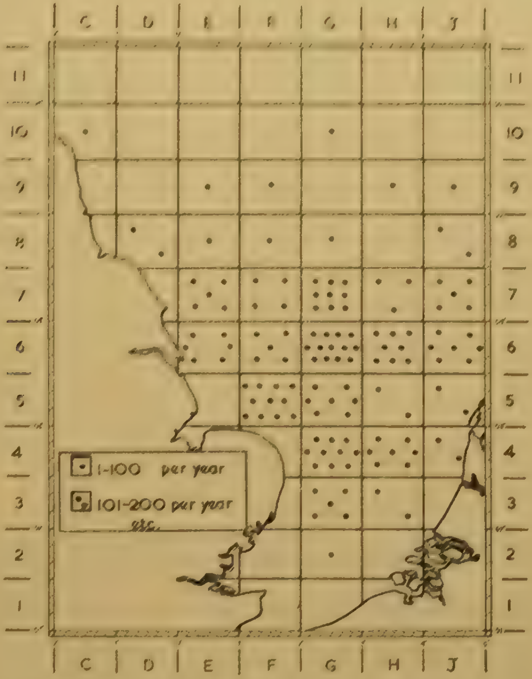

FIG. 15.7 ORIGINS OF PLAICE OTOLITH SAMPLES

[Average number of fish examined from each rectangle per year during period 1946-48.]

In order to compute the value of t_p we need to know with some accuracy the mean date on which recruitment into each age-group occurs, but this cannot be obtained from the pre-war data when samples were taken quarterly. After the war, however, samples were collected monthly, so that we shall first use the post-war (1946-48) data to establish the seasonal pattern of recruitment and the age at which each sub-group is recruited, information which will also be used later in §16.3 in the analysis of the variation in weight among individuals of a given age. When attempting to establish the pattern of recruitment in this way considerable importance attaches to the positions of origin of the samples, particularly their distribution relative to the nursery grounds where the recruitment migration originates. Fig. 15.7 shows the distribution of origin of the otolith samples taken on Lowestoft and Grimsby markets during the years 1945-48, expressed as average numbers of fish examined per year in each rectangle. During analysis of these data it was found that there were no appreciable variations in this distribution between the three years, nor was there much change during each year except that samples originated slightly more to the south-east of the area during the winter months, corresponding with the movement of the fishery at that time towards the plaice spawning area. In addition, it was found that there was a high correlation between the number of fish sampled and the number landed by the fleet from each rectangle, and that the length distribution of the fish in these samples was very similar to that of the fish in the large *random* market samples taken to obtain the length distribution only. For these reasons we may infer that the age-composition of the otolith samples is representative of that of the plaice population in the main area worked by the British trawler fleet.

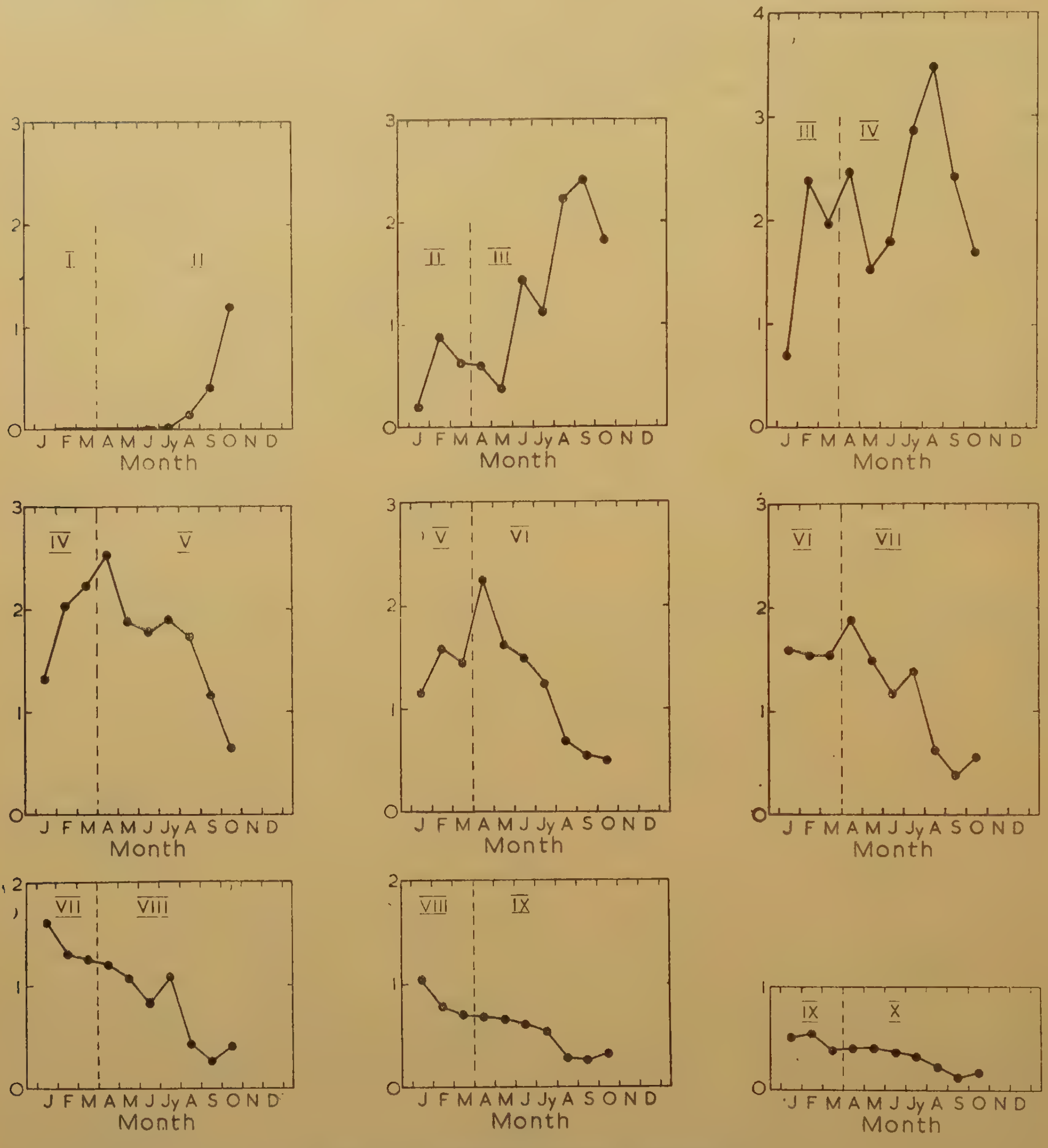

FIG. 15.8 PLAICE RECRUITMENT

[Average number of plaice in each age-group landed each month at Lowestoft and Grimsby per 100 hours fishing by British 1st class steam trawlers, 1946-48; from Table 15.3. There is a marked increase in density of age-groups II, III and IV in the summer, due to recruitment.]

Table 15.3 gives the mean monthly landings of each age-group per 100 hours fishing by British 1st class steam trawlers in 1946-48. When these are plotted (Fig. 15.8), marked differences are seen between the seasonal changes in abundance of certain age-groups. Thus, whereas age-groups I-II, II-III and III-IV show pronounced increases in abundance during the summer months, later age-groups (V-VI and above) show a decline over the same period. Age-group IV-V would seem to be intermediate, in that a steady level is maintained between May and August. At this stage we may conclude that recruitment is restricted primarily to the first three age-groups mentioned, viz. II, III and IV, and occurs during a summer season. These data as they stand do not give the most satisfactory picture of the recruitment pattern, since migrants are continually reduced in numbers by fishing, as well as by natural causes, from the moment they enter the exploited area. This difficulty can be overcome if it is assumed that the mortality of all age-groups when once they have entered the area is the same, in which case we can eliminate the effect of mortality by taking as reference the abundance of age-groups VI and above into which there is no recruitment.* To this end we need to express the numbers of the younger age-groups, II, III and IV in each month as a proportion of the older age-groups VI +, VII + and VIII + respectively, thus obtaining ratios which are independent of the effect of mortality in so far as it is the same in all age-groups. In Table 15.4 these quantities are shown in columns P, Q and R, and smoothed by moving averages of three in columns S, T and U; the smoothed figures are plotted in Fig. 15.9 as if the data referred to the relative abundance of a single year-class during successive years of life. This figure shows clearly the relative increases during the summer of the younger age-groups as a result of recruitment, and it will be seen that there are also apparent decreases in abundance during the winter, but these latter are due to the relative increases in catches of the older year-groups during the intensive winter fishery on the spawning population, and are therefore irrelevant to the present enquiry. Starting with the II-group fish, of which there are none present during the early part of the first recruitment year, our best estimate of the recruitment pattern is obtained by extending the ascending limb of the curve (June-October) to the asymptote (0.5) as indicated in the figure, since if it were not for the spawning migration of the older fish the curve might be expected to remain at the 0.5 level until the next recruitment season begins. Recruitment into age-group III is therefore best represented by drawing the second ascending limb from the level of the previous asymptote as shown, the curve being continued to a second asymptote in the same way. Recruitment into age-group IV is then obtained by the same procedure.

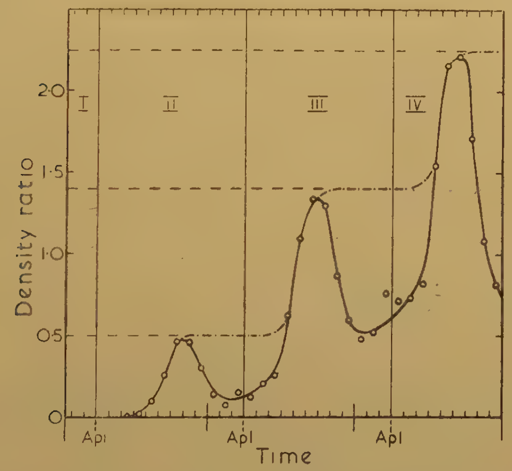

FIG. 15.9 PLAICE RECRUITMENT

[Ratios of densities of age-groups II, III and IV to those of groups VI+, VII+ and VIII+ in each month; from Table 15.4. This procedure minimises the effect of trends and fluctuations common to both young and old fish, and enables recruitment to be measured.]

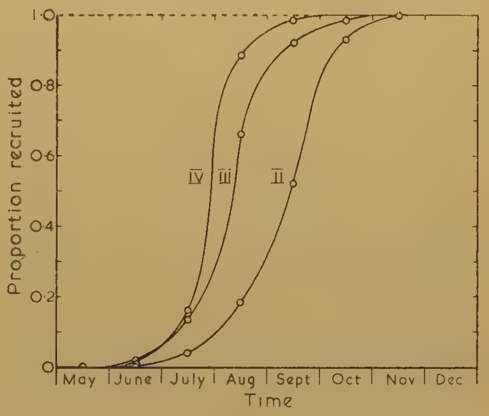

FIG. 15.10 PLAICE RECRUITMENT

[Seasonal recruitment ogives for age-groups II, III and IV constructed from Fig. 15.9, as set out in Table 15.5.]

It is interesting to note in passing that the difference between the first and second asymptotes gives the abundance of group III recruits relative to that of the group II survivors recruited during the previous year. If the difference is therefore reduced by the extent to which II-group survivors have themselves been reduced during the previous year—an estimate of which may be obtained from the data for fully recruited age-groups given in columns M, N and O of Table 15.4—we obtain the abundance of III-group recruits relative to that of II-group fish recruited in the same year. Treating differences between subsequent asymptotes in a similar way gives the relative recruitment into each age-group as defined in §9.3, and hence an estimate of t_ρ. This method would probably be the best way of obtaining t_ρ if data covering a reasonably long period of years, say ten or more, were available; it would then be possible to follow the process of recruitment of each year-class as described above, to estimate t_ρ for each, and then to take the average of as many such estimates as the span of data allowed. For the present data the value of t_ρ obtained in this way from Fig. 15.9 is 3.34 years, but owing to the short period of time involved it is not possible to assess the influence on this value of fluctuations in total recruit numbers during that time. This limitation does not affect, of course, the validity of the seasonal pattern of recruitment deduced from these data, with which analysis we now proceed.

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*It will be appreciated that this procedure is analogous to that used in the analysis of the Leman-Haaks data given in §15.1.2.1.

Values of the relative abundance of recruits in each age-group read off from Fig. 15.9 are given in columns A, B and C of Table 15.5. Subtracting the proportions at the beginning of each recruitment season (the lower asymptotes) from succeeding values (columns D, E and F) and reducing each to an upper asymptote of unity (columns G, H and J), gives the seasonal recruitment ogive for each age-group plotted in Fig. 15.10. These curves show the numbers of fish recruited into each age-group up to any given date, as a proportion of the total number of fish of that age-group which will be recruited during the whole recruitment season. The ogives are roughly symmetrical, and the dates at which each reaches 0.5 can be taken as the mean date of entry of that sub-group of recruits. Consequently the mean age at recruitment of each sub-group is given by the sum of the age-group number and the time interval between April 1st and the mean date of recruitment of that sub-group, expressed as a fraction of a year. These mean ages are given in the following table:

AGE-GROUP	II	III	IV
AVERAGE AGE AT RECRUITMENT (years)	2.45	3.35	4.33

To obtain them has been the main purpose of analysing the post-war data, but the recruitment ogives of Fig. 15.10 have two interesting features worthy of comment at this stage. The first is that the recruitment season is practically coincident with the growing season, and this suggests that the season of growth is also the time of the greatest activity. In the case of a year-class which has not yet reached its equilibrium distribution, a sudden increase in activity would cause it to disperse to a considerable extent within a relatively short time, this change being detectable in the catches of the appropriate age-group from the exploited area. With fully recruited year-classes, that is, those whose distribution has effectively reached its steady state, an increase in general activity would not be manifest in this way. A further link between the phenomena of growth and activity is the fact mentioned in §15.1.2.3 that in those year-classes which have not reached equilibrium it is the fastest growing individuals that are found farthest from the nursery grounds, i.e. which have dispersed to the greatest extent. The second point to note in Fig. 15.10 is that the recruitment seasons of the three sub-groups occur in a chronological order that is the reverse of their ages, and to this extent the process of recruitment to the exploited area is similar to the spawning migration of the older fish, since unpublished information kindly made available to us by our colleague Mr. A. C. Simpson shows that in the mature population it is the older individuals that arrive for spawning before the younger.

We now analyse the pre-war data to obtain estimates of the proportional contribution of each sub-group to the total annual recruitment, and to establish the methods required we shall use the terminology of §§9.3 and 13.1, denoting by ${}_{\theta}\bar{N}_X$ the annual mean abundance of age-group θ in the year X, and by ${}_0R$, ${}_1R$, ... etc. the number of fish in the respective recruit sub-groups, recruited on dates ${}_0t_p$, ${}_1t_p$, ... etc.

We first trace the course of recruitment of a single year-class, and suppose that it first appears in the catch in age-group θ_p during year X. The annual mean abundance of the age-group during this year, assuming the effect of gear selection to be negligible, is then given approximately as

$${}_{\theta_p}\bar{N}_X = \frac{{}_0R}{F+M}\left(1 - e^{-(F+M)(\theta_p + 1 - {}_0t_p)}\right) \quad .. \qquad .. \quad (15.11)$$

The period $\theta_p + 1 - {}_0t_p$ is seen to be the time interval elapsing between the mean date of recruitment of the sub-group ${}_0R$ and the end of the biological year on the following March 31st, and is therefore the fraction of the year X during which the sub-group ${}_0R$ is exposed to the full fishing mortality F. On rearranging (15.11) we have

$${}_0R = \frac{{}_{\theta_p}\bar{N}_X (F+M)}{1 - e^{-(F+M)(\theta_p + 1 - {}_0t_p)}}$$

During the following year $(X + 1)$ the year-class in question will comprise age-group $(\theta_p + 1)$, and its presence in the catch will be made up partly of fish recruited in that year, i.e. the sub-group ${}_1R$, and partly by survivors of sub-group ${}_0R$ which were recruited during year X. The annual mean abundance of age-group $(\theta_p + 1)$ in the year $(X + 1)$ can therefore be written as

$${}_{\theta_p+1}\bar{N}_{X+1} = \frac{{}_1R}{F+M}\left(1 - e^{-(F+M)(\theta_p + 2 - {}_1t_p)}\right) + \frac{{}_0Re^{-(F+M)(\theta_p + 1 - {}_0t_p)}}{F+M}\left(1 - e^{-(F+M)}\right)$$

giving

$${}_1R = \frac{{}_{\theta_p+1}\bar{N}_{X+1}(F+M) - {}_0Re^{-(F+M)(\theta_p + 1 - {}_0t_p)}\left(1 - e^{-(F+M)}\right)}{1 - e^{-(F+M)(\theta_p + 2 - {}_1t_p)}}$$

and in general the number in sub-group ${}_rR$ recruited in year $X + r$ into age-group $\theta_p + r$ is

$${}_rR = \frac{{}_{\theta_p+r}\bar{N}_{X+r}(F+M) - \left(1 - e^{-(F+M)}\right) e^{-(F+M)(\theta_p + r)} \sum_{z=0}^{r-1} {}_zRe^{(F+M)\,{}_zt_p}}{1 - e^{-(F+M)(\theta_p + r + 1 - {}_rt_p)}} \quad .. \quad (15.12)$$

The summation term refers to the total abundance of the survivors from all younger sub-groups.

For analysis of the pre-war plaice age-composition data we use the mean abundance of each age-group of Table 13.1 repeated in row A of Table 15.6, since we have found in §13.2 that the effect of fluctuations in the numbers of annual recruits is virtually eliminated by taking averages for the whole period. As discussed above, we need first to adjust these totals to take some account of the number of fish rejected at sea after introduction of the 23 cm. size limit in 1933. Thus we have obtained from Thursby-Pelham's unpublished data the average number of fish below 23 cm. in each age-group in samples taken between April 1st 1929 and May 31st 1933, and these are presented as a percentage of the total in each age-group in row B of Table 15.6. Adjusting row A by these percentages therefore gives our best estimate of the age-composition of the exploited phase, the result being given in row C. The youngest age-group present is the II-group, so that θ_p of (15.12) has the value 2, and the value of $(F + M)$ for this period has already been determined from the same data (§13.2) viz. 0.83. Finally, the values of ${}_0t_p$, ${}_1t_p$ and ${}_2t_p$, i.e. the mean ages at which recruits enter into age-groups II, III and IV respectively, have been given on p. 260, and we assume in the following calculations that if any recruits enter into higher age-groups they do so on the same date as do the IV-group recruits.

Using these values in (15.12) and putting $r = 2, 3, \ldots$ etc., successively, we obtain the estimates of the magnitude of recruitment into each age-group given in row D, these numbers bearing the same relationship to the actual numbers of recruits as do the figures of row C to the absolute abundance (see §15.2.1 below). The recruitment into each age-group as a proportion of the total annual number of recruits is given in row E and shown as a histogram in Fig. 15.11. The general pattern of recruitment is seen to be similar to that which has been deduced from the Leman-Haaks and post-war plaice data, but it is interesting to note that the present method indicates that there is a small but definite recruitment into age-group V. An estimate of the mean age of the total annual recruits can now be obtained by summing the products of row E and the mean age at which recruitment into each age-group occurs, and gives the value $t_\rho = 3.73$ years.

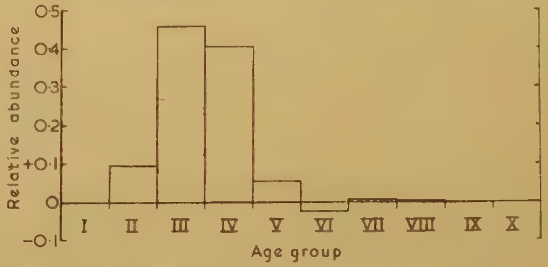

FIG. 15.11 PLAICE RECRUITMENT

[Relative age-distribution of recruits; from Table 15.6. Recruits are mainly of age-groups III and IV, with a small proportion of age-groups II and V.]

15.1.4 *Plaice—construction of resultant selection curves and estimation of mean selection lengths ($L_{\rho'}$) and ages ($t_{\rho'}$) for various mesh sizes*

We have given reasons above for believing that most recruitment in plaice occurs within a size range beyond the selection range of a 70 mm. mesh. In Part IV we shall be concerned with assessing the probable effects of increases in mesh size above this figure, and this will involve the question of the interaction between recruitment and mesh selection as discussed in §8.1.1.4. We showed in that section that in these circumstances the resultant selection curve may be markedly asymmetrical, and that it is therefore better to compute a mean selection age, rather than to take the age at the 50% point, as an estimate of $t_{\rho'}$. In what follows it is more convenient to work with length instead of age as abscissae, to compute a mean selection length and to convert this to age to give the required estimate of $t_{\rho'}$. In plaice the relation between length and age over the limited range of a selection curve is so nearly linear that estimates of $t_{\rho'}$ thus obtained are virtually identical with the true mean selection ages.

The first step is to derive the age-recruitment ogive corresponding to the age-distribution of recruits given in row E of Table 15.6 by taking the cumulative sum of the figures for successive age-groups, the result being given in row F. This ogive can be interpreted as giving the number of fish that have been recruited up to and including those of a given age as a proportion of the total annual recruitment, but in order to combine it with mesh selection ogives it must first be converted to a length-recruitment ogive. This could be done without difficulty if age-composition samples representative of the whole population in the exploited area were available, since the average size of fish in each of the recruit sub-groups could be estimated by the method developed in §16.3. With the present age-composition data, however, rejection of undersized fish from the catch (see §15.1.3) may have had a serious effect on estimates of the average size of fish in the younger sub-groups, even though the number rejected was probably not large enough to have greatly influenced the average age and size of all recruits. For the present purpose we therefore take the mean size of fish in each recruit sub-group as being the same as the mean of all fish of that age. This enables the age-recruitment ogive of row F (Table 15.6) to be converted into length by using the age-length relationship for plaice determined in §16.2.1, the result being tabulated in row G and shown in Fig. 15.12; in column B of Table 15.7 are given the interpolated values of this ogive at each centimetre length.

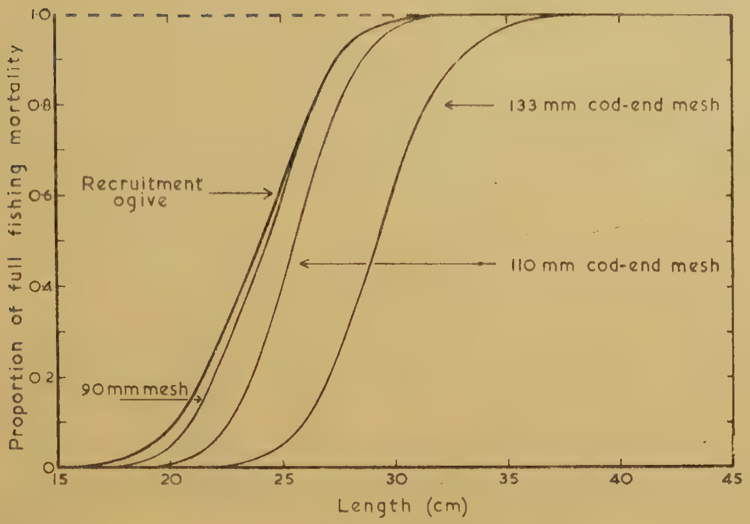

FIG. 15.12 PLAICE RECRUITMENT AND SELECTION

[Recruitment ogive and resultant selection ogives for 90, 110 and 133.5 mm. cod-end meshes ; from Table 15.7. The resultant curves are products of the recruitment ogive and the mesh selection ogive for the mesh in question.]

Turning now to the estimation of $t_{p'}$, it will be remembered from §8.1.1.4 that when the size ranges of recruitment and mesh selection overlap, the probability that a fish of a given length will have entered the exploited phase is given by the product of the ordinates of the recruitment and mesh selection ogives at that length. The latter have been constructed for a number of sizes of cod-end mesh, using the selection factor $b = 2.18$ estimated in §14.2.1. to give the 50% selection length, and representing the spread of the ogives by means of a normal ogive with $\sigma = 2.75$ cm. In order to illustrate the calculation of $t_{p'}$, selection ogives for two very different meshes (70 mm. and 133.5 mm.) are shown in columns C and F of Table 15.7. The products B × C and B × F (columns D and G) therefore give the resultant ogives, and in columns E and H are given the first differences of these ogives. An estimate of $L_{p'}$ for each mesh is given by the sum of the product of these differences and the corresponding lengths (row J). Finally, we need to convert these lengths into age, and for the simple case of constant growth parameters (see below) we obtain the estimates of $t_{p'}$ given in row K. The value of $t_{p'}$ for the 70 mm. mesh is found in this way to be 3.72 years, i.e. effectively the same as that of t_p obtained directly from the recruit age-distribution, and for assessments given later we shall use the values

$$t_p = t_{p'} = 3.72 \text{ years}$$

$$(\text{implying } R = R')$$

to apply to the pre-war plaice population.

In Fig. 15.12 is shown the length-recruitment ogive for plaice, taken from the figures of column B, Table 15.7, together with the resultant selection ogives for 90 mm., 110 mm. and 133.5 mm. meshes, the latter being drawn from column G. The mean selection lengths, $L_{p'}$, for these meshes are given in row J, the full curve of $L_{p'}$ as a function of cod-end mesh size being shown in Fig. 15.13. From this we may read off the value of $L_{p'}$ for a mesh of any size, and it will be used in a number of calculations described in Part IV in which the effects of varying the cod-end mesh size are investigated. In the simple models of Part I, the properties of which are examined in §17, the growth parameters are taken as constant, so that for any given size of mesh there is a fixed relationship between $L_{p'}$ and the corresponding mean selection age $t_{p'}$. The variation of $t_{p'}$ with cod-end mesh size in these circumstances is also shown in Fig. 15.13, the conversion of length to age being accomplished by using the growth parameters determined in §16.2.1. It will be appreciated that this relationship does not hold if we are considering the variation of growth with density, although that between $L_{p'}$ and mesh size is still valid.

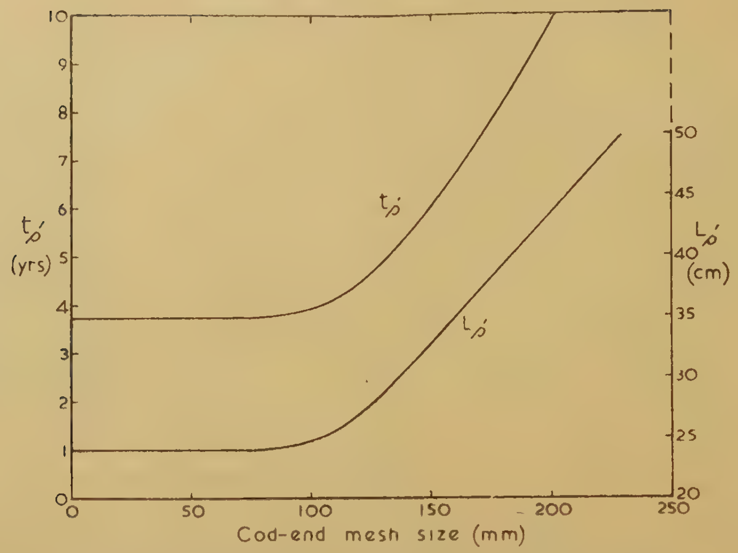

FIG. 15.13 RESULTANT SELECTION IN PLAICE

[Relationship between cod-end mesh and mean selection length (L_ρ') and age (t_ρ').]

15.2 Annual Recruit Numbers and their Relation to Egg-Production

In this section we shall discuss certain questions concerning the absolute number of fish, R, recruited annually to a fish population, starting in §15.2.1 by estimating the mean value of this parameter for plaice and haddock during the pre-war period. This information is used in §15.2.2 to compare the observed variation of the annual yield of each species with that predicted by the methods developed in §6.2, thus providing a basis for the construction of control charts for fishery management (see §19.2.3) and throwing some light on the sampling error of the age-composition data of each species. Finally, in §15.2.3, we examine the relationship between the number of eggs spawned annually by a fish population and the number of surviving recruits, in the few species for which data are available. This leads, in the case of haddock, to deducing a range of possible larval mortality coefficients (see §6.1.1.1) for use in §§18.3.2 and 18.5.2 in self-regenerating population models to examine the consequences of the density dependence of recruitment.

15.2.1 *Estimation of the mean pre-war recruitment* (R) *in plaice and haddock, in absolute units*

It will be remembered that we defined recruitment in §3.1 as the entry of fish into the exploited area at a particular age, t_ρ, though it may be a year or more before the recruits enter the exploited phase. To attempt to estimate R directly, e.g. by marking, will therefore always be difficult and usually impracticable: instead, it is necessary to compute R indirectly from a knowledge of the parameters of the post-recruit phase and some measure of the absolute abundance of the exploited phase, of which the most suitable is the annual yield in weight, Y_W. Thus, if the mortality and growth parameters are known, it is possible to compute the *yield per recruit*, Y_W/R, from (4.4): hence an estimate of the mean value of R for the period in question can be obtained simply by dividing the total yield by the yield per recruit, i.e.

$$\frac{Y_W}{Y_W/R} = R$$

In §17 we give estimates of Y_W/R referring to the pre-war stock of plaice and haddock. Thus for the plaice the figure is

$$Y_W/R = 194 \text{ gm.}$$

corresponding to the pre-war fishing mortality of $F = 0.73$ (see Fig. 17.1). During the years 1929-37 (the period to which this value refers) the average quantity of North Sea plaice landed annually in all European countries was 5.4×10^{10} gm. This includes some catches from places not within the area exploited by British vessels but, on the other hand, does not allow for undersized fish rejected at sea; as a result, the true absolute yield to be related to our estimate of Y_W/R is probably not much different from the figure quoted. Hence the average number of plaice recruited annually to the population we are investigating can be estimated as

$$R = \frac{5.4 \times 10^{10}}{194} = 2.8 \times 10^{8}$$

For the haddock it is found from Fig. 17.24 that the yield per recruit corresponding to the mean pre-war fishing mortality coefficient in this species ($F = 1.0$) and with a cod-end mesh of 70 mm. is

$$Y_W/R = 127 \text{ gm.}$$

During the relevant period (1923-36) the total weight of haddock landed per year from the North Sea by all European countries was 10.8×10^{10} gm., giving

$$R = \frac{10.8 \times 10^{10}}{127} = 8.5 \times 10^{8}$$

These estimates of R refer to the average number of fish reaching the age of recruitment, t_p, which we have taken as 3.72 years in plaice and 1.0 years in haddock. In themselves, estimates of R are not of great interest, but population estimates that are of more general significance can readily be derived from them. In particular, the annual mean numbers of fish in the post-recruit phase, $\bar{P}_N$, can be computed by multiplying the appropriate value of the number per recruit, $\bar{P}_N/R$, obtained from (5.5) by the corresponding value of R. Thus, the value of $\bar{P}_N/R$ for plaice in the pre-war period is 1.205, and multiplying by the above estimate of R gives

$$\bar{P}_N = 1.205 \times 2.8 \times 10^{8} = 3.4 \times 10^{8}$$

Now an independent estimate of the total number of mature plaice that spawned in the Southern Bight of the North Sea in 1948, namely 2×10^{8}, has been made by our colleague Mr. A. C. Simpson (unpublished communication). He based this on estimates of the total number of plaice eggs spawned in that area, the fecundity of plaice, and the size composition and sex-ratio of the mature population estimated from samples of the commercial catch. As it stands, this figure is not directly comparable with that of $\bar{P}_N$ given above; thus the number of mature fish in that year was rather greater than before the war but, on the other hand, it does not include a certain proportion of immature fish that are present in the post-recruit population and contribute to the catch. A more serious difficulty, stressed by Simpson, is that the relative importance of the German Bight spawning is not known accurately but is probably at least half that of the Southern Bight spawning and may be rather more. Thus, starting with Simpson's figure for mature fish in the Southern Bight and taking these factors into account, results in an estimate of between 3 and 4×10^{8} fish in the post-recruit population. Although no more accurate comparison between the two estimates of population size can be made at present, the agreement is nevertheless encouraging, and indicates that there is no serious fault in the picture of the plaice population that we are piecing together by means of theoretical models and data obtained from market samples of the commercial catch.

15.2.2 *The relationship between the variation of recruitment and that of the annual yield*

In §6.2 it was shown that a simple relationship existed between the true variance of recruitment and that of the annual yield, provided it could be assumed that all other parameters were invariable. The relationship in question is (6.31), namely

$$\sigma^2{}_Y \qquad \sigma^2{}_R \sum_{\theta=1}^{\lambda} u^2{}_\theta$$

in which the weighting coefficients u_θ are defined by (6.32) and denote the yield per recruit obtained from each age-group of the exploited phase. It was also suggested in that section that in cases where the effect on the yield of variation in parameters other than recruitment could not be neglected, but was nevertheless small relative to that of recruit variation, it could be represented arbitrarily by means of a residual variance of yield term, ${}_x\sigma_Y{}^2$, which is simply added to or subtracted from the above expression.

It can be seen, therefore, that for predicting the variation in yield corresponding to any specified combination of fishing intensity and mesh size, which may be of importance in fishery regulation and management (see §19.2.3), it is necessary to find the extent to which it can be accounted for by variation in recruitment alone, and also, perhaps, to estimate the residual variance of yield. This we shall do by first obtaining an estimate of the variance of recruitment in plaice during the pre-war period, and then using it to predict the variance of yield during that time by a modification of the above expression containing the appropriate mortality and growth parameters. Finally, this predicted variance of yield will be compared with the value found during the same period from commercial statistics. Incidentally to this investigation we shall show how comparing predicted and observed variances in this way can give useful information about the accuracy and reliability of the sampling methods used to obtain the recruitment estimates.

In the above expression, and throughout this section, the symbol σ^2 denotes true variance; but because successive annual yields are not independent quantities, a variance of yield, $(S^2{}_Y)_q$, observed over a limited period of q years, will tend to be less than the true variance. This *serial dependence* of yield, as we call it, arises from the fact that the year-classes comprising the yield in year X are the same as those in year $X + 1$, with the exception of that which reaches age t_λ at the end of year X and that which enters the exploited phase at the beginning of year $X + 1$. Consequently, the variance of yield predicted from that of recruitment must also be corrected according to the duration of the period to which it refers in order to compare it with an observed value, and we are grateful to our colleague Mr. J. A. Gulland for deducing for us the modified form of (6.31) that is required in this case.

Denoting by $({}_p\sigma^2{}_Y)_q$ the variance of yield predicted from the true variance of recruitment, $\sigma^2{}_R$, over a period of q years, he finds that:

$$({}_p\sigma^2{}_Y)_q = \frac{\sigma^2{}_R}{q-1}\left\{q\sum_{\theta=1}^{\lambda} u^2{}_\theta - \left(\sum_{\theta=1}^{\lambda} u_\theta\right)^2 - Z\right\} \qquad \ldots \quad \ldots \quad (15.13)$$

Z is here a minor correction term that has been evaluated only for the case when the weighting coefficients u_θ are all equal, but this is sufficient for our present purposes since it is always possible to find equal coefficients having nearly the same weighting effect as a given set of varying ones. In this section we need to compute Z with three and four equal weighting coefficients, which we denote by $u_\theta{}'$, the required expressions being:

$$Z_3 = \frac{10\,(u_\theta{}')^2}{q} \text{ (for three equal coefficients)} \qquad \ldots \quad \ldots \quad (15.14)$$

and

$$Z_4 = \frac{28\,(u_\theta{}')^2}{q} \text{ (for four equal coefficients)} \qquad \ldots \quad \ldots \quad (15.15)$$

In §15.1.3 we showed that plaice recruitment occurred mainly in age-groups III and IV, with a small proportion in age-groups II and V. For this species the term 'recruitment' as used above must therefore be interpreted as meaning the 'effective recruitment' in each year, i.e. the total number of fish recruited in one year from the four year-classes II-V, and the symbol R_X must be substituted for R in the above expressions (see §6.2). To estimate the value of R_X for each year it is therefore necessary to estimate the number of fish recruited each year into each age-group. Strictly speaking, this should be done by applying (15.12) to each year-class separately, but we have found it sufficient to apply the average proportional recruitment into each group given in row E of Table 15.8 to the data for each year. By this means an estimate of R_X can be obtained for each of the nine years 1929-37, whereas by using (15.12) only six values could be obtained since only six year-classes are fully represented in the recruit age-groups II to V. From the age-composition data of Table 13.1, adjusted for fish below 23 cm. by the percentages given in row B of Table 15.6, we estimate in this way the variance of effective recruitment to be

$$S^2_{R_X} = 0.67 \times 10^7$$

in the same units as those of Tables 13.1 and 15.6, i.e. 'nos. per 100 hrs. fishing'. To convert this to absolute units it is necessary to multiply by the square of the ratio of the mean effective recruitment (in the same units, i.e. $R_X = 6{,}792$) to the mean absolute recruitment estimated in §15.2.1, (i.e. 2.8×10^8). Thus we have, in absolute units,

$$S^2_{R_X} = \left(\frac{2.8 \times 10^8}{6.792 \times 10^3}\right)^2 \times 0.67 \times 10^7 = 1.08 \times 10^{16}$$

Values of u_θ for the plaice, calculated from (6.32) using values of growth and mortality parameters for the pre-war period given in this paper, are tabulated in column B of Table 15.8. The damping effect of this series of u_θ is not more than would result from four equal coefficients, so that to compute Z of (15.13) we use (15.15) with

$$u_\theta' = \frac{1}{4}\sum_{\theta=1}^{\lambda} u_\theta = 48.87 \text{ gm.}$$

By inserting the above values of $S^2_{R_X}$, u_θ and u_θ' in (15.13), and with $q = 9$, it is now possible to compute an estimate, $({}_pS^2{}_Y)_q$, of the true predicted variance of yield $({}_p\sigma^2{}_Y)_q$. It is only an estimate because it contains the estimated variance of recruitment, $S^2_{R_X}$, and not the true variance, $\sigma^2_{R_X}$, and this distinction is important at a later stage. It is

$$({}_pS^2{}_Y)_q = 5.75 \times 10^{19} \text{ gm.},$$

while the observed variance of the annual European yield of plaice from the North Sea for the same nine years is

$$(S^2{}_Y)_q = 4.52 \times 10^{19} \text{ gm.}$$

Thus our prediction of the variance of yield is some 25% greater than the observed value, but before discussing the implications of this result, mention needs to be made of the statistical significance that can be attached to it. Ordinarily, two estimates of the variance of a population—using the term in the statistical sense—say from two random samples, will differ by chance. In the present case, however, the 'predicted' and 'observed' variances of yield are not independent, since they both derive from nearly the same set of annual recruitments. It is true that the observed variance of yield depends not only on the variance of the recruit broods, but also on their chronological order, and that certain year-classes contribute to the yields at the beginning of the series but do not appear in the set of recruit values. But in spite of this it seems reasonable to proceed on the supposition that the predicted and observed variances of yield obtained above do differ significantly.

The first question is whether the observed variance of yield is likely to be affected appreciably by variation of factors other than recruitment. Now, if the effects of changes in the latter tend to be in the same direction as those in the yield itself, or if they are independent of the direction of changes in the yield, the observed variance will be greater than if all parameters other than recruitment were constant; while changes in a direction such that they tend to oppose the changes in yield due to the remaining factors, will be compensatory and tend to reduce the variation of yield. Although no precise assessment of the resultant effect of these influences on the actual variation in yield of plaice can be made, the indications are that changes were not only small but were also of both kinds, each thus tending to counteract the other's effect. The weight-at-age data given in Table 16.2, for example, show small fluctuations largely independent of changes in yield, though some compensation must have occurred because it is known that the growth of North Sea plaice is inversely related to population density, and hence, indirectly, to yield. Changes in fishing intensity also seem to have been small, judging by the rough indices of European effort given in Table 14.15. Certainly, there is no evidence of compensation in these data, neither were the changes in abundance or distribution of plaice during the period likely to have been large enough to have resulted in much variation in searching power, i.e. in the relation between effort and effective overall fishing mortality coefficient (see §10.3). On balance, there seems no reason for the observed variation of yield to be appreciably different from the value expected if all factors other than recruitment were truly constant.

Turning now to the predicted variance of yield, $({}_pS^2{}_Y)_q$, it can be seen at once that it includes the effect of errors involved in estimating the true variance of recruitment.* That part of the total variance of recruitment due to this cause we term *observational error variance;* its composition depends to some extent on the method of obtaining the recruit estimates (e.g. whether by market or research vessel sampling), but it always includes the random variation inherent in any sampling process, and also any errors arising from irregularly biased or otherwise faulty sampling.

The resultant effect of these various factors influencing the observed and predicted variances of yield is best demonstrated symbolically, as follows. The observed variance of yield over q years, $(S^2{}_Y)_q$, can be regarded as consisting of the variance due to fluctuations in recruitment and that due to fluctuations in all other parameters (the 'residual' variance), i.e.,

$$(S^2{}_Y)_q = (\sigma_Y)_q + ({}_x\sigma^2{}_Y)_q \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (15.16)$$

The predicted variance of yield, $({}_pS^2{}_Y)_q$, computed from (15.13) using the estimated variance of recruitment, $S^2{}_{RX}$, consists partly of true predicted variance and partly of variance due to observational error in the recruit estimates. Denoting the latter by $\sigma_{\varepsilon RX}$, we therefore have:

$$({}_pS^2{}_Y)_q = \sigma^2{}_{RX}\ \phi(u_\theta) + \sigma^2{}_{\varepsilon RX}\ \phi(u_\theta) \quad \ldots \quad \ldots \quad \ldots \quad (15.17)$$

where $\phi(u_\theta)$ denotes the function of u_θ appearing in full in (15.13). But $\sigma^2{}_{RX}\,\phi(u_\theta)$ of (15.17) is by definition identical with $(\sigma^2{}_Y)_q$ of (15.16), so that subtracting (15.16) from (15.17) gives

$$({}_pS^2{}_Y)_q - (S^2{}_Y)_q = \sigma^2{}_{\varepsilon RX}\ \phi(u_\theta) - ({}_x\sigma^2{}_Y)_q \quad \ldots \quad \ldots \quad \ldots \quad (15.18)$$

It can therefore be seen that if we know the magnitude of either the observational error variance of the recruit estimates, or the residual variance of yield, then an estimate of the other can be computed from the difference between the predicted and observed variances of yield.

In the present case, an investigation of the sampling methods used to obtain the plaice age-composition data has recently been completed by Gulland (1955a), and indicates that observational error in the pre-war data probably resulted in a coefficient of variation of the order of 20% for the estimated number of fish in a given age-group. It is therefore instructive to find how nearly this agrees with that computed from (15.18) assuming that the residual variance is zero. On rearranging, (15.18) gives

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*Strictly speaking, the observed variance of yield may also include an error component, but this must be very small and can be neglected here since the yield is not a sampled quantity but is wholly measured.

$$\sigma^2_{\varepsilon R_X} = \frac{({}_pS^2{}_Y)_q - (S^2{}_Y)_q}{\phi(u_\theta)}$$

in which all quantities on the right hand side are known. Thus using the values given above, we find

$$\sigma^2_{\varepsilon R_X} = \frac{(5.75 - 4.52) \times 10^{19}}{5{,}326} = 0.23 \times 10^{16}$$

Now this is the error variance of the estimates of effective recruitment, R_X, but each value of R_X is composed of fish belonging to several age-groups. This results in the variance of R_X being less than that of the true recruitment, R, and less than that of the number of fish in each age-group. That part of the total variance of R_X due to error will therefore be similarly damped relative to the error variance of the original age-composition data. Some allowance for this can be made by applying (6.34) to these error variances, i.e.

$$\sigma^2_{\varepsilon R} = \sigma^2_{\varepsilon R} \sum_{r=1}^{\Phi} p_r^2$$

where $\sigma^2_{\varepsilon R}$ denotes the error variance of the true recruitment (which can be taken as equivalent to that of the original age-composition data), and p_r denotes the proportion that the rth recruit sub-group is of the whole recruited year-class. Values of p_r are given in row E of Table 15.6, and from the above expression we find

$$\sigma^2_{\varepsilon R} = 2.56 \times \sigma^2_{\varepsilon R_X} = 0.59 \times 10^{16}$$

so that

$$\sigma_{\varepsilon R} = 0.77 \times 10^8$$

Now the mean recruitment has been estimated in §15.2.1 as $\bar{R} = 2.8 \times 10^8$; hence the coefficient of variation due to observational error estimated in this way is

$$\frac{\sigma_{\varepsilon R}}{\bar{R}} \times 100 = \frac{0.77 \times 10^8}{2.8 \times 10^8} \times 100 = 27\%$$

Bearing in mind the indirect method of arriving at this estimate of the 'error' in the age-composition data, agreement with the figure obtained by direct analysis is good; indeed, the two almost certainly do not differ significantly. Hence nearly all the difference found above between the estimates of predicted and observed variances of yield can be attributed to observational error in measuring effective recruitment, and the residual variance of yield would seem small enough to be neglected. This result suggests that predictions of variation in yield from the plaice fishery can be made with some confidence. The agreement found between estimates of observational error made by two methods is also important, because although direct statistical analysis of the market sampling process is, on the whole, the more satisfactory method, there could be certain kinds of bias not readily detected by it, yet which contribute to the discrepancy between predicted and observed variances of yield.

With the above points in mind, it is interesting also to compare the observed and predicted variance of yield in haddock. The recruit estimates in column R of Table 15.9 have a variance of

$$S^2{}_R = 6.83 \times 10^{17}$$

while values of u_θ for the pre-war haddock population are given in column C of Table 15.8.

These decrease in magnitude more rapidly than do those of column B for plaice, and for the purpose of estimating Z of (15.13) we use (15.14) with

$$u_0' = \frac{1}{3}\sum_{\theta\;\;1}^{\lambda} u_\theta = 42.25 \text{ gm.}$$

With $q = 16$, the predicted variance of yield computed from (15.13) is

$$({}_pS^2{}_Y)_q = 36.31 \times 10^{20} \text{ gm.}$$

whereas the observed variance of the European haddock yield during the same period is

$$S^2{}_Y = 6.67 \times 10^{20} \text{ gm.}$$

With a predicted variance so much larger than the observed one it is difficult to escape the conclusion that the 'observational error' of the haddock recruit estimates is at least as large as the true variance of recruitment, and possibly several times greater. This result has an important bearing on the interpretation of relationships between recruitment, egg-production and environmental factors in the haddock; a problem that is discussed in the following section.

15.2.3 *Estimation of egg-production and of pre-recruit mortalities*

15.2.3.1 *Plaice*

Despite the extensive investigations that have been carried out on North Sea plaice by a number of workers, it so happens that the amount of suitable data concerning the relationship between egg-production and subsequent recruitment in this species is small. Thus, although egg-production has been measured directly by Hensen net sampling in a number of years prior to the 1939-45 war (Buchanan-Wollaston, 1923), only recruitment from the 1927 spawning falls within the period covered by the age-composition data of Table 13.1. Again, the fact that a year-class of plaice is not fully represented in market samples until its fifth year of life, means that only six pairs of values of egg-production, E, and recruitment, R, can be obtained from Table 13.1, using the fecundity data published by Simpson (1951a). With so few points, the variation in abundance of the mature population (and hence in E) compared with that in the values of R, was found to be far too small for any correlation of R with E to be distinguished. Another possible approach was to see whether the immediate post-war recruitments were significantly greater than before the war,since they were the progeny of a war-time stock whose abundance had increased several-fold (Margetts & Holt, 1948). The size of post-war recruitments, however, is bound to have been affected by the intensive fishery that developed during the war on the younger age-groups on or near to the nursery grounds, so that their abundance in post-war market samples is not readily comparable with pre-war data.

Although there seem, then, to be insufficient data for a detailed analysis, it is probably not without significance that such evidence as is available, including that from samples of the nursery stock such as the Leman-Haaks surveys (e.g. Thursby-Pelham 1928, 1932), gives no indication that the large changes in abundance of mature plaice during the last fifty years have had any clearly-defined influence on recruitment. This suggests that, in harmony with the model represented by (6.10), there is an upper limit to the number of plaice recruits, and that egg-production has so far always been sufficient to maintain recruitment near to that asymptote. In Part IV we shall therefore assume that, over the range of population size we need to consider, plaice recruitment is effectively independent of the abundance of the spawning population.

15.2.3.2 *Haddock—the problem of predicting recruitment*

The haddock age-compositions of Table 13.2, on the other hand, cover a longer series of years and a wider range of population abundance than do the plaice data. Moreover, recruitment in haddock can be regarded for practical purposes as restricted to one age-group. For these reasons we use the haddock data in this section as a basis for discussing some of the problems that arise when investigating the relationship between egg-production and recruitment, including the estimation of larval mortality coefficients, while certain of the results will be used in Part IV to illustrate the properties of self-regenerating models.

For indices of recruitment we have followed Raitt (1939) in using the catch per 10 hrs. fishing of I-group fish. Recruits from the 1922-36 year-classes are obtained from Table 13.1 to which we have added a figure for the 1937 year-class kindly supplied by Mr. B. B. Parrish of the Scottish Marine Laboratory. The mean of these values is 1063, to be compared with the mean recruitment in absolute units of 8.5×10^8 estimated for the same period in §15.2.1. The indices of abundance of I-group fish in each year must therefore be multiplied by the factor

$$\frac{8.5 \times 10^8}{1063} = 8.0 \times 10^5$$

to convert them to absolute numbers of recruits at age $t_\rho = 1$ year, and these products are entered in colum R of Table 15.9 against the year in which they were spawned.

To estimate the egg-productions of which these recruits were the progeny we have used data on the size, fecundity and attainment of maturity in haddock published by Raitt (1933), together with the age-compositions of Table 13.2. The first step is to obtain estimates of the age-composition on the average date of spawning, which we have taken as April 1st. Raitt's Table 2, from which our Table 13.2 is derived, gives the mean abundances between 1st April and the following 31st March, and abundance at spawning time can be obtained with sufficient accuracy by taking the average of the mean abundances of the appropriate year-classes during the year before and the year after a given spawning date. These are given in columns B to H of Table 15.9.

Table 15.10 shows the derivation of factors needed to convert these abundance figures into estimates of the egg-production of each year-class at each age. The proportion of females in each age-group we have taken as 0.5 (column B), while the fraction, p, of female fish that have matured by the end of each year of life is given by Raitt (ibid, p. 30), and is tabulated in column C. The fecundity factors χ—in the units *no. of eggs shed per season per gm. body weight*—have been obtained from Raitt's data and are given in column D. The mean weight of fish at the end of each year of life, computed from the age-weight relationship for haddock given in §16.2.2, is tabulated in column E.

The final step is to derive a factor to convert estimates of abundance at spawning time (columns B to H, Table 15.9) into absolute units. Now the mean recruitment figure of 8.5×10^8 refers to instantaneous abundance at age $t_\rho = 1$ year, but the indices of recruitment refer to mean abundance during the second year of life. Hence the factor 8.0×10^5 used previously includes, in effect, an adjustment to take this difference into account; the adjustment is, in fact, the annual mean abundance of fish (during their second year of life) per recruit entering the age-group on its first birthday, $(\bar{P}_N/R)_I$. This can be computed by means of (5.5), using parameter values appropriate to the pre-war haddock population, and is

$$\left(\frac{\bar{P}_N}{R}\right)_I = 0.9$$

with sufficient accuracy. Hence the factor needed to convert indices per 10 hrs. fishing to absolute units, when the former already refer to instantaneous abundance (as do the data of columns B to H) is nine-tenths of the previous factor, i.e. 7.2×10^5. The products of this and columns B to E of Table 15.10, give the factors of column F by which indices of abundance in columns B to H of Table 15.9 are multiplied to give the annual egg-production at each age, entered in columns J to P. Finally, these have been summed in column Q to give the total egg-production in each year, being those from which survived the recruits given in the corresponding row of column R.

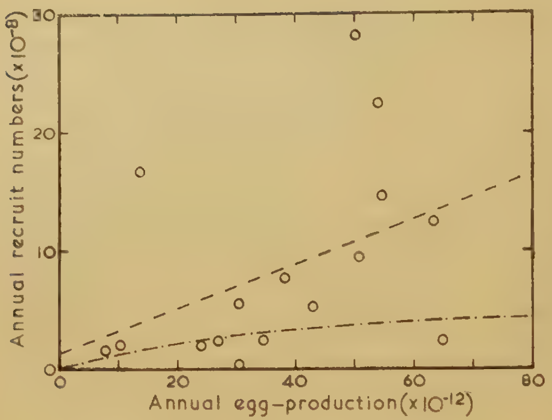

FIG. 15.14 EGG-PRODUCTION AND RECRUITMENT IN HADDOCK

[Recruitment plotted against corresponding egg-production during period 1922-38; from Table 15.9, columns Q and R. The fitted linear regression is shown as – – –, and the curve given by (6.10) as – · – · with $\bar{\alpha} = 1.53 \times 10^{-9}$, $\bar{\beta} = 61{,}400$.]

It is clear that the number of recruits fluctuates very greatly. The question is to find how much this is due to fluctuations in egg-production. The data of columns Q and R are plotted in Fig. 15.14, and it is seen that there is some tendency for higher values of R to be associated with higher values of E. The linear correlation coefficient is

$$r = 0.417$$

and testing the significance of this by the Z-test gives

$$z = 0.444$$

with a standard error of $+ 0.277$. The data are not therefore highly correlated and variation in egg-production can account for only about one-fifth of the total variance of the recruitment estimates. On the other hand, comparison between the predicted and observed variances of haddock yield in §15.2.2 suggested that most of the observed variation in the recruit estimates could be due to observational error. Remembering also that some variation is bound to arise through fluctuations in the larval mortality rate, it can be seen that even if the true values of E and R were perfectly correlated one would not necessarily expect a much larger value of r than that found above. Moreover, it is doubtful whether with sixteen points such a value would be statistically significant. Yet another reason why a high value of r is unlikely is that the true relationship between E and R is probably curvilinear.

Bearing the above points in mind, the correlation between recruitment and egg-production shown in Fig. 15.14 is perhaps as good as could be expected, and while it is clear that the data cannot be used to distinguish critically between the various theoretical representations of pre-recruit mortality developed in §6.1.2, certain general statements can nevertheless be made. There is no definite evidence, for example, of recruitment reaching a maximum within the observed range of egg-production (in contrast to Herrington's data for the Georges Bank haddock mentioned in §15.2.3.3). This suggests that the relationship might conform more nearly to the type represented by (6.10), in which recruitment tends asymptotically to an upper limit with increasing egg-production. It will be remembered that such a relationship, which we believed to be the most general of those put forward in §6.1.1.1, results from postulating a linearly density dependent natural mortality rate during part or all of the pre-recruit phase, and is defined by two derived mortality parameters, α and β. In order to investigate (in §§18.3.2 and 18.5.2) the properties of self-regenerating population models in which recruitment varies with egg-production, we shall therefore use (6.10) and a range of pairs of values of α and β that are not inconsistent with the haddock data of Table 15.9.

Now it was shown in §6.2 that the most probable mean yield over a period of time is predicted from models containing the mean recruitment, $\bar{R}$, during that time. For investigating steady states the required pairs of α and β are therefore those that give the most probable value of $\bar{R}$ associated with a given value of the mean egg-production $\bar{E}$. Hence they should satisfy the equation

$$\bar{R} = \frac{1}{\alpha + \beta/\bar{E}}$$

in which $\bar{R}$ is the mean recruitment in an observed steady state, and $\bar{E}$ is the mean egg-production computed for that steady state from an appropriate expression such as (6.21), containing appropriate values of the mortality, fecundity and growth parameters, and converted to absolute units by means of the value of $\bar{R}$ in question. For haddock, our estimate of the latter is $\bar{R} = 8.5 \times 10^8$, while the corresponding value of $\bar{E}$ computed from (6.21) is 1.47×10^{13}. A range of pairs of α and β consistent with these figures that will be used in self-regenerating population models discussed in §§18.3.2 and 18.5.2 is as follows:

$\alpha \times 10^9$	β	Curve of Fig. 15.15
0.937	3,500	(p)
0.835	5,000	(q)
0.494	10,000	(r)
0.289	13,000	(s)
0.085	16,000	(t)

The corresponding *E-R* curves are shown in Fig. 15.15. The assumption of a constant recruitment is shown, for comparison, by the broken horizontal line (a).

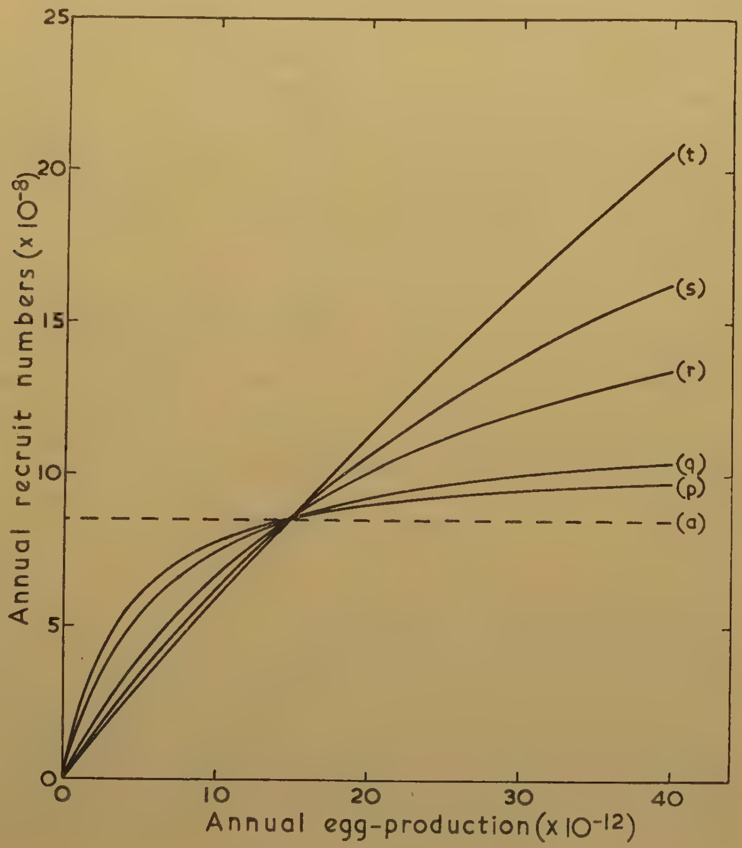

FIG. 15.15
EGG-PRODUCTION AND RECRUITMENT IN HADDOCK
[Some examples of possible curves relating egg-production and recruitment in haddock constructed from (6.10) with values of α and β given on p. 273. These are used in self-generating models in §18 to investigate the effect of making recruitment vary with egg-production.]

As has been mentioned above, with so great a variation in R the data are too few to permit a fit of (6.10) in the usual sense, although we shall show in §18.5.2 how some restriction of the possible range of α and β may be obtained. Now the principles underlying the fitting of curves to data by methods such as that of least squares require any departures of individual points from the theoretical curve to be regarded as due to errors, or at least to disturbing factors whose influence is to be minimised. Admittedly, some of the differences between the points of Fig. 15.14 and the theoretical curves are due to sampling error, but some are also due to real differences in the larval mortality rate, which we may express in terms of differences in the values of α and β. Instead of attempting to minimise the variation of the points of Fig. 15.14 by fitting (6.10) and finding a single pair of values of α and β, an alternative procedure is to regard each value of R as being generated by a different pair of values of α and β, the variation in R (and hence in E) being due to real variations in α and β. With this approach the parameters we need to determine from the data of Table 15.9 are the mean values $\bar{\alpha}$ and $\bar{\beta}$, and we may proceed as follows.

By rearranging (6.10) we have

$$\alpha = \frac{1}{R} - \frac{\beta}{E}$$

and

$$\beta = E\left(\frac{1}{R} - \alpha\right)$$

and summing both sides of each equation gives

$$n\bar{\alpha} = \sum\frac{1}{R} - \sum\frac{\beta}{E} \quad \cdots \quad \cdots \quad \cdots \quad (15.19)$$

and

$$n\bar{\beta} = \sum\frac{E}{R} - \sum\alpha E \quad \cdots \quad \cdots \quad \cdots \quad (15.20)$$

where n is the total number of pairs of observed values of E and R. Now if neither α nor β is correlated with E, and certainly there is nothing in the way these coefficients are derived to suggest that such a correlation is likely, then $\bar{\alpha}\sum E$ can be used as an unbiased estimate of $\sum\alpha E$, and, similarly, $\bar{\beta}\sum 1/E$ as an estimate of $\sum\beta/E$. By making these substitutions in (15.19) and (15.20) respectively, $\bar{\alpha}$ may be eliminated, giving

$$\bar{\beta} = \frac{n\sum\frac{E}{R} - \sum E\sum\frac{1}{R}}{n^2 - \sum E\sum\frac{1}{E}} \quad \cdots \quad \cdots \quad \cdots \quad (15.21)$$

whence $\bar{\alpha}$ is obtained by substituting this value of $\bar{\beta}$ in either of the above equations. From the data of Table 15.9, with $n = 16$, we find by this method

$$\bar{\alpha} = 1.53 \times 10^{-9}$$

and

$$\bar{\beta} = 61{,}408$$

and the resulting curve is shown as — . — . in Fig. 15.14.

The above values of $\bar{\alpha}$ and $\bar{\beta}$ are those which predict the value of R that would result from a particular value of E if α and β were of average magnitude; that is to say, they are the values which would give the best year to year prediction of the size of a future year-class from a knowledge of the contemporary adult population (i.e. the contemporary value of E).*

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*Strictly, the most probable value of R would be predicted in this way only if the distributions of α and β were symmetrical, but in the absence of any information on this point a tacit assumption of symmetry is the best that can be made in the circumstances.

It would, however, be incorrect to use these values in our deterministic population models with which we predict the most probable steady state involving a relationship between a steady egg-production and a constant recruitment. For this purpose the data must be treated as if α and β were constants, not stochastic variables; hence departures from the fitted curve are regarded as errors and the former method of fitting is used.

The above methods are relevant to a problem that has received considerable attention in recent years, namely that of tracing the relationship between the fluctuations in recruit brood strength and in certain environmental factors. Fundamentally, the problem is one of relating the magnitude of the larval or pre-recruit mortality rate for each brood to the corresponding environmental conditions, and the parameters whose values are to be thus correlated are therefore α and β—or some other appropriate measures of mortality rate.* It is not possible, of course, to determine values of both α and β from a single observation, and it would be necessary to have some idea of which parameter would be most likely to be affected by each environmental factor in question, as discussed in §6.1.1.1. For example, Carruthers, Lawford, Veley and Parrish (1951) have stated that the direction of the prevailing winds bears some relationship to the strength of year-classes in North Sea haddock, the mechanism suggested by these authors being that winds from certain directions cause young larvae to be carried out of the normal nursery areas and be lost to the population. In this case we might expect that a given direction and strength of wind would cause roughly the same percentage mortality whatever the initial number of eggs, that is, it would be essentially a density-independent effect (Burkenroad, 1951) and could be represented by variations in the magnitude of the μ_1 coefficients and hence in the values of β. A possible procedure would therefore be to suppose that each recruit value had been generated by the same value of the coefficient μ_2, of which an estimate could be obtained from $\bar{\alpha}$ and β as defined above, and to represent individual values of R in terms of those of E and the appropriate values of β. The latter could then be examined for correlation with the environmental factor in question, or better, made the basis of a multiple regression analysis using as many as possible of the factors believed to influence primarily the μ_1 coefficients. In this connection it is worth noting that Davidson and Andrewartha (1948) have successfully applied the multiple regression technique to an essentially similar problem, namely that of analysing the variance of estimates of the mean size of an insect population into observational errors, the effects of various physical factors of the environment, and dependence on the size of the previous generation.

The procedure adopted by Carruthers *et al*, (ibid) for haddock, and by Carruthers, Lawford and Veley (1951) for other North Sea species including plaice, is to correlate recruit numbers themselves with a single environmental factor (wind strength and direction at spawning time). The results thus obtained are very striking, but in certain respects are difficult to reconcile with the results of the investigation into the variation of recruit estimates for plaice and haddock given above. Their procedure is, of course, the only possible one if egg-production is unknown and if data for only one environmental factor are available; but in this case there is almost certain to be a large residual variance due to the sum of the effects of other environmental factors influencing larval mortality (such as food supply, see §6.1.1.1), as well as to observational error in both the recruit estimates and those of the environmental factor in question. In addition, unless recruitment is very near to an asymptotic limit, egg-production must also contribute to variance of the recruitment estimates. In other words, the best possible correlation between estimated recruit numbers and estimates of any one environmental factor can scarcely be expected to be a very good one, any more than can that between estimates of recruit numbers and egg-production alone (see above).

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*When attempting to relate the severity of the larval mortality in each year to the corresponding environmental conditions, the parameters whose values are to be thus correlated are those of α and β *for each year*—or some other appropriate measures of larval mortality. In practice any value of α or β obtained by these methods will refer to the whole pre-recruit phase whose duration may often be greater than a year. Grant (1952) gives results which may be used as the basis for tests of randomness in a series in which each observation depends on average conditions over a period of time longer than the interval between observations. Her methods might also have application to problems of analysing year to year variations in mortality coefficients and in the interpretation of control charts for yield (see §19.2.3).

Now the correlations between estimates of recruit numbers and wind functions obtained in the species examined by these authors are so high that they seem incompatible with the above remarks, and in particular, with the probable amount of observational error in the recruit estimates. The lowest correlation is in the haddock; but even here only some 10-20% of the total variance of the recruit estimates (which are based on the same data as are those of Table 15.9) is left to represent the variance due to all the other factors mentioned above, and the size of the observational error variance alone is probably several times greater than this (see §15.2.2). In the plaice, the 'correlations' obtained (see Carruthers, Lawford and Veley, 1951, Fig. 10) are nearly perfect, and the residual variances virtually nil; yet in any correlation between plaice recruit estimates and one environmental factor the residual variance must be at least two-fifths that of the total, since this is the fraction due to observational error (see §15.2.2).

The explanation of this anomaly, in the plaice at least, is that the appropriate wind function and values have been arrived at, in the absence of any other information, by finding those that gave the best correlation with the recruit estimates, or in other words, that resulted in the smallest residual variance. The danger of this procedure is that it can easily lead to an apparent correlation being obtained, even if the factor in question has no effect whatever on brood strength. This has been demonstrated more fully by Gulland (1953), who has also pointed out the corollary; namely, that with a correlation obtained in this way it is impossible to assess the likelihood of it having arisen by chance. Thus the fundamental objectivity of the normal correlation technique as a research tool is lost, and there is no way of knowing what degree of confidence should be put in the result as a basis for prediction or future investigations. The method of arriving at the wind function used in the haddock is not stated in full, but the residual variance is probably not so small that it need throw doubt on wind being a factor influencing brood strength. In the plaice, however, the extremely small residual variance can only imply that the correlation claimed is as much with errors in estimating recruit numbers as with true brood strengths, and the result cannot therefore be used as a firm basis for prediction.

15.2.3.3 *Egg-production and recruitment in some other species*

Because of the great importance of the relationship between egg-production and subsequent recruit numbers in determining the reaction of a fish population to exploitation (Herrington, 1944) it is worth reviewing briefly some of the published data of this kind in the light of the theoretical concepts put forward in §6.1.1.1.

Tester (1948, Fig. 7) has shown the relationship between an index of spawning potential and the relative number of subsequent recruits for the British Columbia herring (*Clupea pallasii*), and in Fig. 15.16 we show a graph of Tester's data. There is no evidence of a trend here, so we could presume that the *E-R* curve is virtually at its asymptotic level within the range of egg-production covered by the data (which is the conclusion reached by Tester) and hence that the u_2 coefficients are primarily responsible for the larval mortality which has occurred. It is interesting to find that the coefficients

$$\alpha = 0.0031$$

$$\beta = 0.0031$$

produce a curve (full line) similar to the freehand curve drawn by Tester (broken line). These two curves are shown in Fig. 15.16, but it is clear that these particular data can give no indication of exactly where the bend takes place, and the asymptote may be effectively reached at a much lower level of egg-production than Tester has indicated by the point X. In fact, determining $\bar{\alpha}$ and $\bar{\beta}$ by means of (15.21) gives the values

$$\bar{\alpha} = 0.075$$

$$\bar{\beta} = -0.043$$

which result in a convex curve, though the value of $\bar{\beta}$ is not significantly negative.

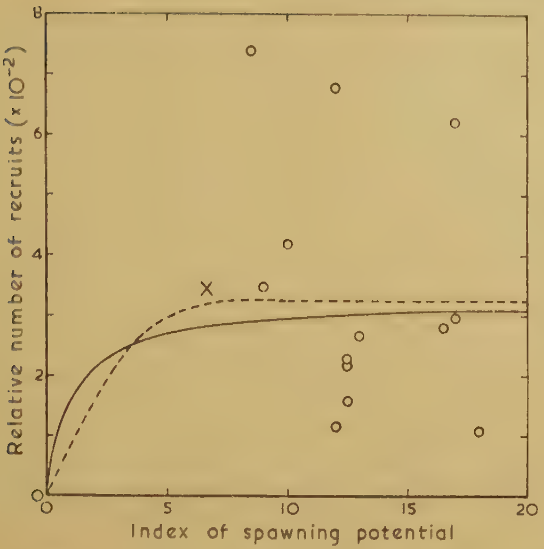

FIG. 15.16 EGG-PRODUCTION AND RECRUITMENT IN BRITISH COLUMBIA HERRING

[Relationship between spawning potential and recruitment, from Tester (1948). The broken line is the freehand curve drawn by Tester; the full line is the curve given by (6.10) with $\alpha = \beta = 0.0031$.)

The natural propagation of various species of Pacific salmon has been studied in great detail and is relevant in the present connection. A convenient summary of data for the sockeye (*Oncorhynchus nerka*) of Cultus Lake has been given by Foerster (1944, Table IV), while data for the coho (*O. kisutch*) and the pink (*O. gorbuscha*) have been published by Pritchard (1947, Tables II and III), giving the potential egg-deposition in certain years and the percentage efficiency of propagation, i.e., the number of subsequent fry expressed as a percentage of the potential egg-deposition. We have used the percentage efficiency figures to estimate actual numbers of fry—which can be regarded as equivalent to the recruitment—and the resulting figures are shown in Fig. 15.17. Unlike the previous cases we have considered, there is now a very clear relationship between R and E, and in each case the points do not appear to depart much from a straight line. This would suggest that egg-production is far from the 'saturation level', and that we are dealing with parts of $E-R$ curves relatively near to the origin where larval mortality is determined effectively by the μ_1 coefficients. As in the case of Tester's data, we cannot obtain good values of $\bar{\alpha}$ and $\bar{\beta}$ from Fig. 15.17 (though here it is because the observed points are few and lie below the region of greatest curvature), but it is interesting to find that in all cases but one (Beadnell Creek, coho), estimates of $\bar{\alpha}$ and $\bar{\beta}$ obtained from (15.21) give lines that have appreciable curvature within the range of the data, and are neither extremely steep nor nearly horizontal. These curves and the corresponding values of $\bar{\alpha}$ and $\bar{\beta}$ are shown in Fig. 15.17.

Rounsefell (1949) has presented a long series of data of total run and escapement for the Fraser River sockeye salmon, which we have used in §14.3.2.2 to illustrate a method for separating the natural and fishing mortality coefficients. If we assume that escapement is proportional to egg-deposition these data can be used to show the $E-R$ relationship in this population, and the total run in each year is plotted in Fig. 15.18 against the escapement four years previously.* Again there is definite indication of a trend, and by (15.21) we obtain the values

$$\bar{\alpha} = 1.03 \times 10^{-7}$$

$$\frac{\bar{\beta}}{sf} = 0.160$$

where s is the proportion of female fish in the escapement and f the number of eggs laid by each.

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*Rounsefell has shown that there are four-year cycles of abundance in this population, owing to the fact that the greater part of the total run of each year is comprised of a single year-class. In the present case, however, it did not seem necessary to distinguish the $E-R$ relationship for each of the four cycles and they are combined in Fig. 15.18.

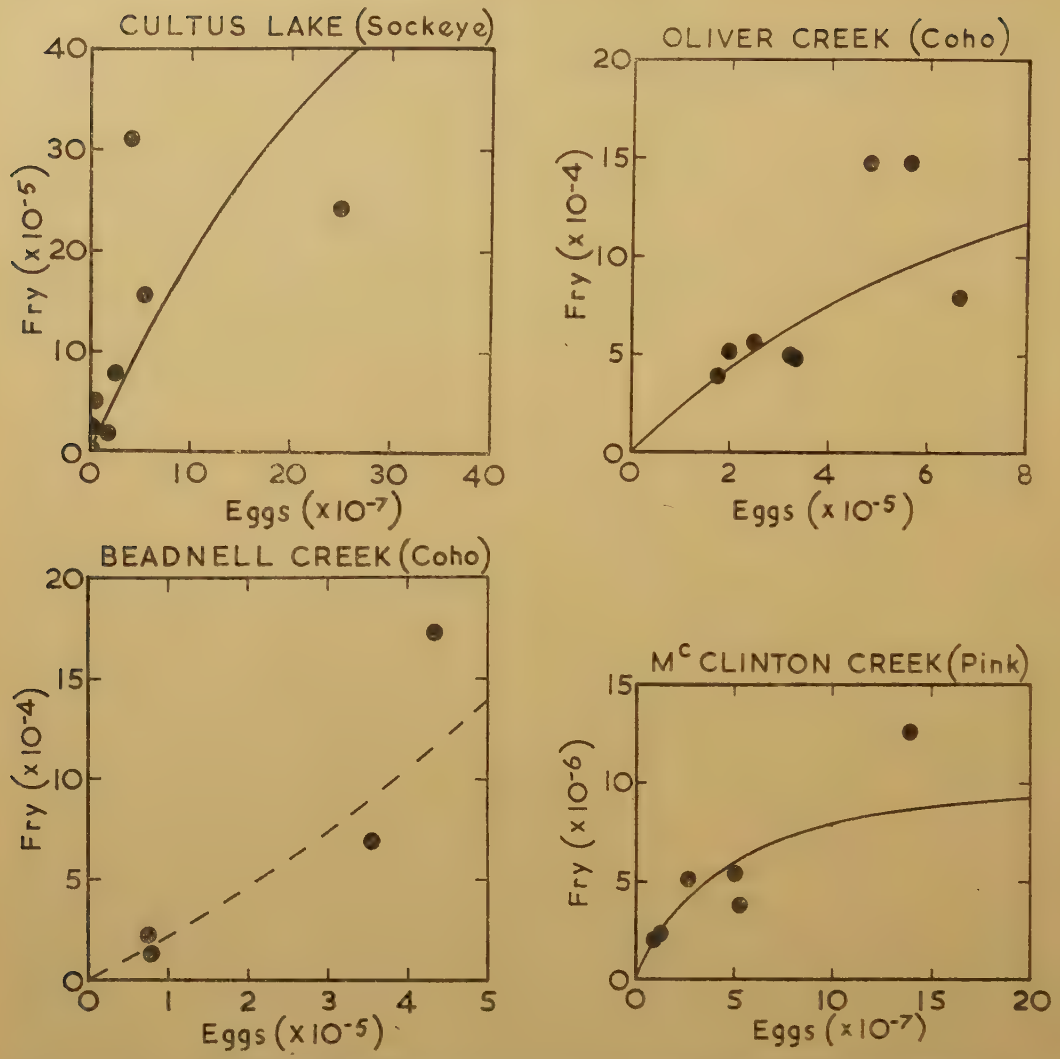

FIG. 15.17 EGG-PRODUCTION AND RECRUITMENT IN PACIFIC SALMON

[Relationships between egg-deposition and numbers of fry; data from Foerster (1944) and Pritchard (1947). The curves are obtained from (6.10) with values of $\bar{\alpha}$ and $\bar{\beta}$ as follows:

Cultus Lake (sockeye)	$\left\{\begin{array}{l}\bar{\alpha} = 0.91 \times 10^{-7} \\ \bar{\beta} = 42.4\end{array}\right.$	Oliver Creek (coho)	$\left\{\begin{array}{l}\bar{\alpha} = 0.37 \times 10^{-5} \\ \bar{\beta} = 3.86\end{array}\right.$
Beadnell Creek (coho)	$\left\{\begin{array}{l}\bar{\alpha} = -0.28 \times 10^{-5} \\ \bar{\beta} = 4.93\end{array}\right.$	McClinton Creek (pink)	$\left\{\begin{array}{l}\bar{\alpha} = 0.87 \times 10^{-7} \\ \bar{\beta} = 4.13\end{array}\right.$

The resulting line is shown in Fig. 15.18. A point of interest here is that scatter of the R values increases markedly as E increases over the first part of the range, and this seems in accordance with what would be expected from the theoretical treatment of §6.1.1.1 which implies that density-independent factors (represented by the μ_1 coefficients) are the main cause of larval mortality when egg-production is relatively small. We would emphasize that we have not tested any of the above estimates of $\bar{\alpha}$ and $\bar{\beta}$ for significance, but it is worth noting that of the seven examples we have considered so far, five give values of $\bar{\alpha}$ and $\bar{\beta}$ that result in a concave curve (the exceptions being the British Columbia herring and the coho salmon of Beadnell Creek).*

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*It should be noted that some of the above examples of the relation between egg-production and recruitment have also been discussed by Ricker (1954 a, b), whose theoretical interpretation differs in certain respects (see also §6.1.1.2, p. 60).

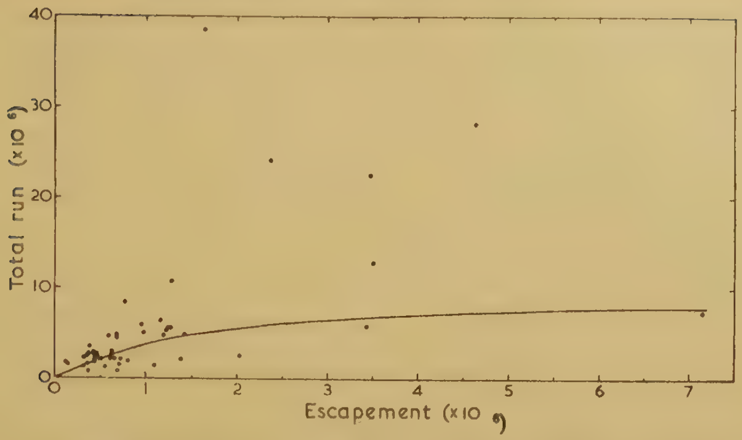

FIG. 15.18 EGG-PRODUCTION AND RECRUITMENT IN FRASER RIVER SALMON
[Relationship between escapement and total run; data from Rounsefell (1949). The curve is obtained from (6.10) with $\bar{\alpha} = 1.03 \times 10^{-7}$, $\beta = 0.160$.]

SECTION: 16 GROWTH AND FEEDING

In the development of the theoretical population models of Parts I and II, von Bertalanffy's equation was used to describe the change in weight of a fish with age. After first considering briefly, in §16.1, the relationship between weight and length in fish,and particularly in plaice and haddock, we show in §16.2 that the weights-at-age for both species are adequately represented by the von Bertalanffy equation (3.7) and discuss a method of fitting it to data. For this purpose we have used data referring to the mean weight of fish at each age, but the analysis of recruitment in plaice given in §15.1.2 indicated that variation in weight among individuals of a given age may be of considerable importance in this species. In §16.3 the analysis is therefore taken a little further, and we discuss ways in which that variation may be represented in terms of the growth parameters K and W_∞. Finally, in §16.4, we consider the question of the relationship between growth, population density and food consumption, dealing first with observed changes in growth and corresponding changes in density of the plaice and haddock (§16.4.1). In §16.4.2, physiological data on growth in plaice are analysed to obtain estimates of the parameters defining the relationships between growth and food consumption that appear in the population models of §9.4.3.

16.1 THE RELATIONSHIP BETWEEN WEIGHT AND LENGTH

It will be remembered that a formulation of the relationship between weight and length is required in the development of the von Bertalanffy equation. In its differential form, viz.:—

$$\frac{dw}{dt} = Hs - Dw \quad .. \quad .. \quad .. \quad .. \qquad (16.1)$$

the question of whether growth is isometric does not arise, but to solve this we need to express both the 'surface area', s, and the weight, w, in terms of the linear dimension, l. In §3.4 this was done by assuming isometric growth and a constant specific gravity so that we could write

$$s = pl^2 \quad .. \quad .. \quad .. \quad .. \quad .. \qquad (16.2)$$

and

$$w = ql^3 \quad .. \quad .. \quad .. \quad .. \quad .. \qquad (16.3)$$

Now, whereas the constant p refers purely to the shape of the organism, q is the product of the specific gravity and a 'space' factor which, if l is identified with the overall length of the organism, is the fraction of the volume of a cube of side l that the organism would occupy.

A discussion of allometric growth is outside the scope of the present paper, but it is clear that such a phenomenon cannot be considered apart from the representation of the process of growth itself. Thus if (16.1) were used, it would seem desirable that the relationship between weight and length should be expressed in a way that can distinguish between changes in form and changes in specific gravity. For example, if the latter changed as length increased, but the body form remained constant, we should expect (16.3) to require modification but not necessarily (16.2). Allometric growth, on the other hand, whether accompanied by changes in the specific gravity or not, would render both (16.2) and (16.3) invalid, so that the solution of the original differential equation above would be different in the two cases.

Early workers on problems of growth and form in fishes, e.g. Meek (1903), Fulton (1904) and Russell (1914), were content to use (16.3) with l defined as the overall length of the fish from nose to tail, and they appreciated the dual nature of the constant q. They found, in general, that this method gave a good representation of the relationship between weight and length, though the value of q showed seasonal variations and sometimes varied slightly with age, and its value for a given size group came to be used as a measure of the 'condition' of the fish. A minor refinement of a statistical nature was made to (16.3) by Wallace (1911), following Heincke, which took account of the difference between the average of the cubes of the individual lengths of fish in a sample and the cube of the average length.

After Huxley's (1924) application of the allometric formula $y = bx^k$ to describe the relative growth of various parts of the body, an analogous form relating weight and length, viz.

$$w = bl^k \quad .. \quad .. \quad .. \quad .. \quad .. \quad (16.4)$$

has been applied to the growth of fish by a number of authors, and the simple cubic has come to be used less frequently and in some cases criticised adversely. Certain authors, notably Hile (1936), have stressed the empirical nature of (16.4) and the care with which it must be used for studying changes in condition, while Kesteven (1947b) has proposed a method for distinguishing changes in volume from changes in specific gravity. We must therefore consider briefly the relative merits of (16.3) and (16.4) from the point of view of our present requirements.

As far as the purely empirical representation of data is concerned, (16.4) is superior to (16.3) because there is freedom to adjust the values of two parameters instead of one, but in that case there is no special significance to be attached to (16.4) as opposed, for example, to a general polynomial which could give a still better representation. It so happens that when (16.4) is fitted, the values of b and k thus found may vary within wide limits for very similar data, and are sensitive to what may be quite unimportant variations in the latter.* Serious errors may therefore arise if the fitted expression is used to extrapolate beyond the range of the data or if introduced into a theoretical population model.

The second question concerns the formal implication of (16.4). The exponent k bears no simple relation to the dimensions of the animal unless it is exactly 3; it may be regarded as the ratio of the two relative growth rates, i.e. $(dw/w\,dt)/(dl/l\,dt)$, as Richards and Kavanagh (1945) have pointed out. Correspondingly, the constant b of (16.4) no longer has the simple interpretation of the constant q of (16.3), and as these authors (p. 198) have said . . . . . . "The complexity of the dimensions of b make interpretation extremely difficult and hazardous". This is a serious limitation from our point of view, since it means that if we relate weight to length by means of (16.4) we cannot distinguish the effects of a change in specific gravity from those of true allometric growth, so that the theoretical requirements for the integration of the von Bertalanffy equation cannot be met (see also von Bertalanffy, 1949). There are other fundamental objections to the use of the allometric growth formula (16.4) which are fully discussed by Reeve and Huxley (1945) and do not require mention here. It would therefore seem that for our purposes the allometric weight-length formula introduces more problems than it solves, and bearing in mind that examples of important departure from isometric growth in adult fishes are rare, it seems that the simple cubic relationship (16.3) is in general the most satisfactory one for incorporation in our theoretical population models.

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*Writers such as Richards and Kavanagh (1945) and Reeve and Huxley (1945) have stressed the need for an adequate statistical approach to the problem of fitting (16.4), but to our knowledge in only three cases in which (16.4) has been fitted to weight-length data in fishes has the significance of a difference between the value of k thus found and the value 3 been tested (Frost, 1945, Martin, 1949 and LeCren, 1951).

There are no published data of the weights and lengths of plaice in the inter-war period and from the area to which our weight-at-age data given in §16.2.1 refer, though the observations of Meek and Fulton cited above were of plaice and they showed that weight and length in this species were adequately related by a simple cubic expression. However, a large number of length and gutted-weight measurements were obtained from this area in 1946, and these are summarised in columns A, B and C of Table 16.1, the average weight at each centimetre length being plotted in Fig. 16.1. In column D of Table 16.1 are given the theoretical values of weight at each length obtained from the fitted cubic equation

$$w = 0.00892\, l^3$$

the corresponding curve being shown in Fig. 16.1. It will be seen that the fit is not exactly true since deviations occur in sequence on the same side of the theoretical curve, but the discrepancies between observed and predicted values are very small and it is clear that the simple cubic expression gives a representation of the weight-length relationship in this species good enough for our purpose. A value of

$$q = 0.00892$$

for the plaice will therefore be used in subsequent calculations in this paper.*

Raitt (1933) has used the allometric formula (16.4) in the analysis of weight and length in haddock, and found that k was slightly greater than 3, though this appeared to be due largely to the anisometric growth of the ovaries. Raitt was mainly concerned with investigating the fecundity of the haddock and its relation to body size, so that his sample consisted only of females and was taken at the spawning season (March) when the ovary

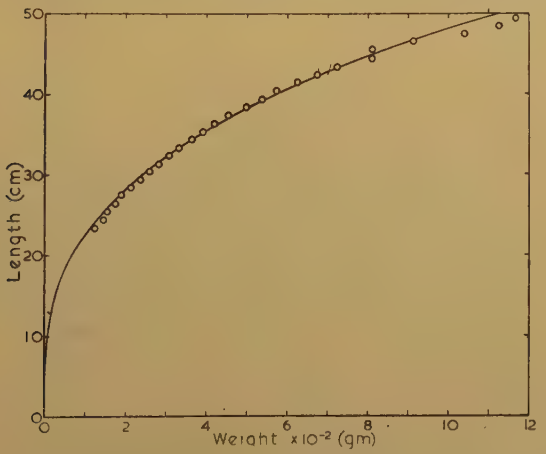

FIG. 16.1
THE WEIGHT-LENGTH RELATIONSHIP IN PLAICE
[The curve is that obtained from the simple cubic equation $w = 0.00892\, l^3$ fitted to the data of Table 16.1.]

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*Fitting (16.4) to the data of Table 16.1 gives the values

$$b = 0.00775$$

and

$$k = 3.04$$

but we have not tested the significance of k compared with the value 3 nor have we investigated whether any changes in specific gravity occur as the length increases in the plaice.

would be most fully developed. We might expect to find that representative sampling of both males and females during the course of a year would yield data which would be fitted more closely by a simple cubic expression. We know of no other recent published data of weight and length in haddock, but by dealing throughout with 'cleaned' weights, that is gross body weight less gut and gonads, we can take into account the data given by Russell (1914). For the calculations of this paper we therefore use the value

$$q = 0.00812$$

derived from Russell's data and the summaries given by Raitt.

16.2 Estimation of the Parameters of the von Bertalanffy Growth Equation

It will be remembered that for the simple population models of Part I we assumed that the growth pattern is constant, or specifically, that growth could be described by the von Bertalanffy equation containing parameters whose values are constant. It has already been noted that both the plaice and haddock populations were in a fairly stable condition during the greater part of the inter-war period, and since most values of the parameters determined so far refer to these years it is appropriate that we should use the corresponding weight-at-age data to estimate parameters of the von Bertalanffy equation for use in the Part I population models. We deal first with the plaice.

16.2.1 *Plaice*

Table 16.2 gives the average weight of plaice in each age group landed by British trawlers from the Southern North Sea during each of the sampling years 1929-38, together with mean values for the whole ten-year period. There is no obvious trend in the yearly figures and consequently the summarised data in the last row of the table have been taken as the best estimates of the average weight-at-age of plaice in the population under investigation over this period, and they are plotted in Fig. 16.2 (circles). The samples from which these data were obtained are the same as those from which the age-compositions of Table 13.1 were computed except that no March or April samples are included; consequently the average weight of each age-group has been related to an age equal to the age-group number plus a period a little greater than 0.5 years, which we have taken as 0.7 years.

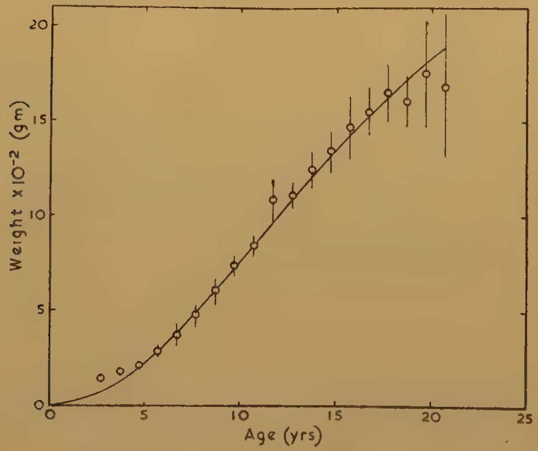

FIG. 16.2
GROWTH IN WEIGHT OF PLAICE

[Average weight of fish in each age-group from Lowestoft and Grimsby market samples, 1929-38. The curve is obtained by fitting the von Bertalanffy equation (see text and Figs. 16.3 and 16.4), with parameter values $W_\infty = 2867$ gm., $K = 0.095$, $t_0 = -0.815$ yrs. The length of each vertical line is equal to six times the standard error of the corresponding mean. From Tables 16.2 and 16.3.]

It will be seen that the general shape of Fig. 16.2 is that of a continuous asymmetrical sigmoid curve, having an inflexion between 500 and 1000 gm., and possibly tending to an asymptote between 2000 and 3000 gm. These characteristics will be recognised as in general agreement with the requirements of the von Bertalanffy equation (see §3.4), and the method we have used to fit it to weight-at-age data is as follows. It is first written in a form linear in $w_t^{1/3}$, thus

$$w_{t+1}^{1/3} = W_\infty^{1/3}(1 - e^{-K}) + w_t^{1/3}\, e^{-K}$$

where w_t is the weight at any age t, and w_{t+1} is the weight one year later. In Table 16.3 the cube roots of the weights at each age are given in column C and successive pairs are plotted in Fig. 16.3. It will be seen that the points are well represented by a straight line, with the exception of the first two and possibly the last two. The latter are based on very small numbers of observations, but this is not the case with the first two points.

In the analysis of the recruitment migration of plaice (§15.1.2) we have shown that all II-group fish and the majority of III-group fish present in the population which we were sampling were recent recruits, and that there are reasons for believing that they were bigger than the average size of the whole year-class to which they belonged. Further support to this conclusion is given below and in §16.3. In Fig. 16.3 the best straight line has therefore been drawn without reference to the first two points; the slope, which is e^{-K}, gives a value of

$$K = 0.095$$

while its point of intersection with the bisector drawn through the origin gives a value of

$$W_\infty^{1/3} = 14.206$$

so that

$$W_\infty = 2867 \text{ gm.}$$

It should be noted here that this technique is essentially the same as that developed by Ford (1933), who first showed that the curve of growth in length of fish (herring was the species in question) could be expressed in a linear form by plotting length at age t against length at age $t + 1$. This method of transforming the growth curve, the mathematical basis of which is, in effect, the same as that of von Bertalanffy's equation for growth in length, was later developed independently by Walford (1949b), who showed that it could

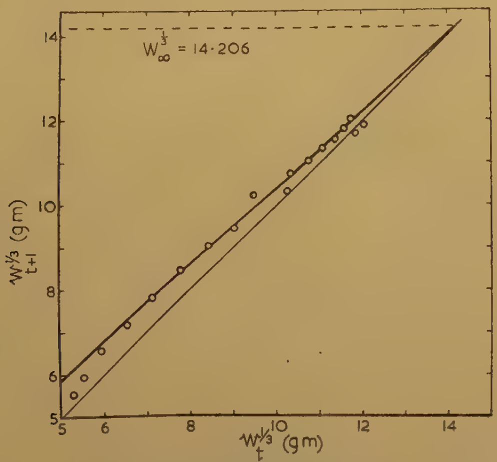

FIG. 16.3 METHOD OF FITTING THE VON BERTALANFFY EQUATION TO DATA

[First stage; plot of $w_{t+1}^{1/3}$ against $w_t^{1/3}$. Where the best straight line through these data cuts the bisector through origin is where $w_{t+1}^{1/3} = w_t^{1/3}$, i.e. is an estimate of $W_\infty^{1/3}$. The slope of the line gives an estimate of e^{-K}. See Table 16.3, column B.]

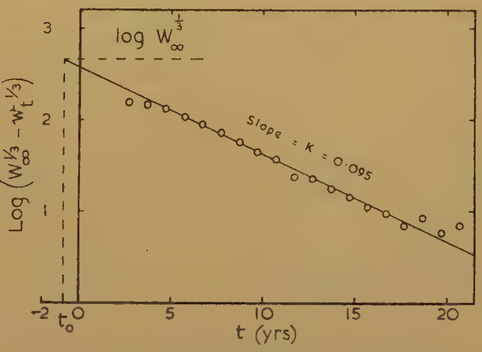

FIG. 16.4 METHOD OF FITTING THE VON BERTALANFFY EQUATION TO DATA

[Second stage; plot of log $(W_\infty^{1/3} - w_t^{1/3})$ against t. The slope of the line gives an estimate of K and the value of t where it has an ordinate of log $W_\infty^{1/3}$ is an estimate of t_0. See Table 16.3, column E.]

be applied successfully to growth data of a number of species of fish. Thus in all the examples given by Walford, the growth curves could be well represented by the von Bertalanffy equation.

The theoretical age, t_0, at which the weight of the fish is zero, remains to be determined. The equation may be written in a form linear in t (see von Bertalanffy, 1938), viz.:

$$\log (W_\infty^{1/3} - w_t^{1/3}) = \{\log (W_\infty^{1/3}) + Kt_0\} - Kt$$

Values of $\log (W_\infty^{1/3} - w_t^{1/3})$, obtained using the value of W_∞ determined above, are tabulated in column E of Table 16.3 and plotted against the corresponding age in Fig. 16.4, giving

$$\log W_\infty^{1/3} + Kt_0 = 2.576$$

and hence

$$t_0 = -0.815$$

It will be noted that the slope is $-K$, and from Fig. 16.4 we again find that $K = 0.095$.

The theoretical weights at each age can then be calculated; these are given in column F of Table 16.3 and the theoretical growth curve is shown in Fig. 16.2. The scatter of the weight-at-age data in Table 16.2, and also that for other species presented below, is sufficiently small that it seemed unnecessary to attempt a rigorous statistical analysis. The fitting of curves which tend to an asymptote has received little attention hitherto, but a paper by Stevens (1951) discusses the problem in detail and may be consulted where a more rigorous method of fitting is needed.

To find the weights of the youngest age-groups, which are not fully represented in the population we are sampling, we have made use of the data from the Leman-Haaks line of stations referred to in §15.1.2.1. The analysis of the distribution of younger fish given in the previous section indicated that even from this line of stations completely representative sampling of those age-groups may not have been obtained but, nevertheless, the data are far superior—for this purpose—to the market samples which we have been using above. Table 16.4 gives estimates of weight-at-age derived from the length data of Wallace (1907, Table 5) and Thursby-Pelham (1932, Tables 20 and 21), using the length to weight

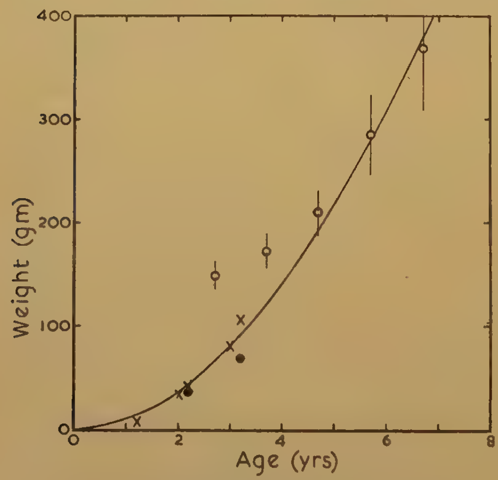

FIG. 16.5

GROWTH IN WEIGHT OF YOUNG PLAICE

[Lower part of the von Bertalanffy curve of Fig. 16.2 drawn on a larger scale to show fit of additional data for plaice younger than those present representatively in market samples. X = Wallace (1905), ● = Thursby-Pelham (1932), ○ = points shown in Fig. 16.2.]

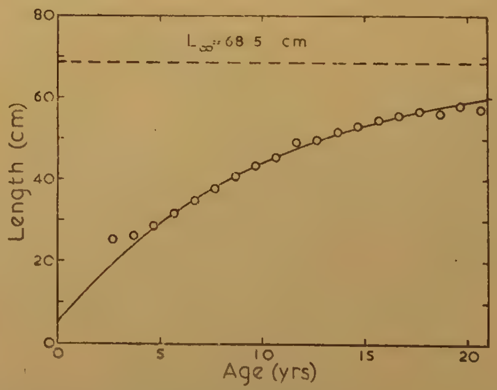

FIG. 16.6 GROWTH IN LENGTH OF PLAICE

Average length of fish in each age-group from Lowestoft and Grimsby market samples, 1929-38. The curve is obtained by fitting the von Bertalanffy equation with parameter values $L_\infty = 68.5$ cm., $K = 0.095$, $t_0 = -0.815$ yrs.; from Table 16.3, columns G and H.]

conversion method of Wallace (1911). These weights are plotted in Fig. 16.5 and it will be seen that they fall close to the theoretical curve, thus justifying our exclusion of the values for II and III-group fish of Table 16.2 when fitting the growth curve.

It was necessary when dealing with mesh selection in plaice to use the von Bertalanffy expression for growth in length, and further need will arise in Part IV. The value of L_∞ required in this equation is given by the cube root of the ratio W_∞/q, so that

$$L_\infty = \sqrt[3]{\frac{2867}{0.00892}} = 68.5 \text{ cm.}$$

The theoretical curve of Fig. 16.6 for growth in length of plaice is obtained by plotting values of

$$l_t = L_\infty \left(1 - e^{-K(t - t_0)}\right)$$

using this value of L_∞ and the values of K and t_0 found above, and it will be seen that it fits well the points obtained by converting weight-at-age data to lengths (see also colums G and H, Table 16.3).

16.2.2 *Haddock*

At the time this investigation was undertaken we were unable to find any detailed published data for weight-at-age of the North Sea haddock during the inter-war period to which the age-compositions of Table 13.2 refer. Raitt (1939, Table 7) gives data of length-at-age during certain years, but these refer to sub-areas and to the first four years of life only. For this paper we shall therefore use the summarised estimates of length at the end of each year of life given by Raitt (1933, p. 37), and these are given in column B of Table 16.5 and plotted in Fig. 16.7.

The von Bertalanffy equation can be fitted to lengths in a way similar to that described above for cube roots of weight, and plotting l_{t+1} against l_t from Table 16.5 gives the estimate

$$L_\infty = 53.0 \text{ cm.}$$

The second stage is to plot log $(L_\infty - l_t)$ against t, giving a straight line of negative slope from which we estimate

$$K = 0.20$$

$$t_0 = -1.07 \text{ years}$$

The fitted curve using these values is shown as the continuous line in Fig. 16.7, the theoretical lengths at the end of each year of life being given in column C of Table 16.4. From Raitt (1939, Table 7) we have obtained an estimate of the length of one-year-old fish—marked with an asterisk in Table 16.5—and it will be seen that it falls close to the theoretical curve.

Finally, in columns D and E of the same Table, are given the estimated and theoretical weights of cleaned fish derived from the lengths in column B and C respectively by means of the equation

$$w = 0.00812\, l^3$$

The estimated weights, together with the theoretical curve of growth in weight, are shown in Fig. 16.8, the latter being calculated using a value of

$$W_\infty = q\, L_\infty^3 = 1209 \text{ gm.}$$

16.2.3 *Other species and discussion*

It is clear that the von Bertalanffy equation represents the growth pattern of plaice and haddock with considerable accuracy, but in order to bring out certain of its interesting biological implications we shall consider briefly data for two other North Sea populations,

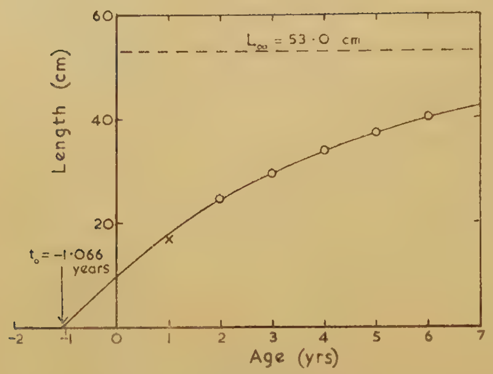

FIG 16.7

GROWTH IN LENGTH OF HADDOCK

[Average length of certain age-groups and the fitted von Bertalanffy curve with parameter values $L_\infty = 53$ cm., $K = 0.20$, $t_0 = -1.066$ yrs.; from Raitt (1933, 1939) and Table 16.5.]

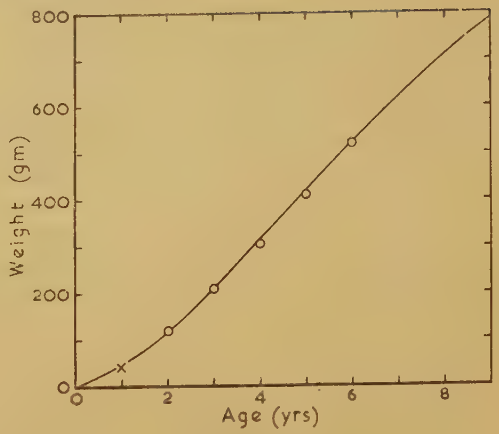

FIG. 16.8

GROWTH IN WEIGHT OF HADDOCK

[Length data of Fig. 16.7 converted to weight and the fitted von Bertalanffy curve with parameter values $W_\infty = 1{,}209$ gm., $K = 0.20$, $t_0 = -1.066$ yrs.; from Table 16.5, columns D and E.]

namely the cod (*Gadus callarias* L.) and the sole (*Solea vulgaris* Quensel), which differ very greatly in their rate of growth.

For the cod we use summaries of the modal length at each age given by Graham (1934, p. 67) which are tabulated in column B of Table 16.6, and give

$$L_\infty = 132 \text{ cm.}$$

$$K = 0.20$$

$$t_0 = 0.28 \text{ yrs.}$$

We find from the extensive weight-length data given by Russell (1922, App. F) that a simple cubic equation with

$$q = 0.00869$$

gives a good representation of the relationship between weight and length in this species. With this value of q we have calculated the weights corresponding to the modal lengths, and these are given in column C of Table 16.6. From the above value of L_∞ we also find

$$W_\infty = 20{,}000 \text{ gm.}$$

The theoretical curve of growth in weight and the calculated weights of column C are shown in Fig. 16.9, and it is interesting to find that the great difference between the growth of cod and haddock, two closely related species, can be represented in the von Bertalanffy equation purely by a difference in W_∞, the values of K being identical within the limits of accuracy of the data and very different from the value of 0.095 found for plaice.

Buckmann (1934, Fig. 5) has published growth data for North Sea sole, the observed length (mean of males and females) on each birthday being given in column B of Table 16.7. Fitting the von Bertalanffy equation gives the parameter values

$$L_\infty = 37.7 \text{ cm.}$$

$$K = 0.42$$

$$t_0 = 0.3 \text{ yrs.}$$

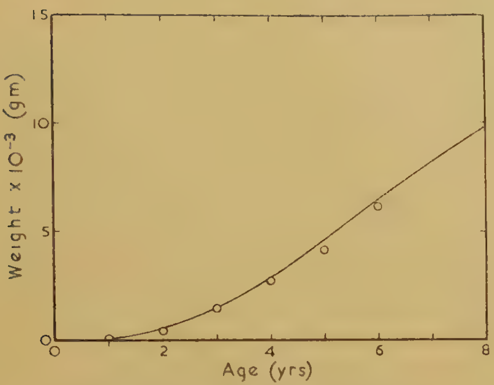

FIG. 16.9 GROWTH IN WEIGHT OF NORTH SEA COD

[Length data from Graham (1934) converted to weight, and the fitted von Bertalanffy curve with parameter values $W_\infty = 20{,}000$ gm., $K = 0.20$, $t_0 = 0.28$ yrs.; from Table 16.6, columns C and D.]

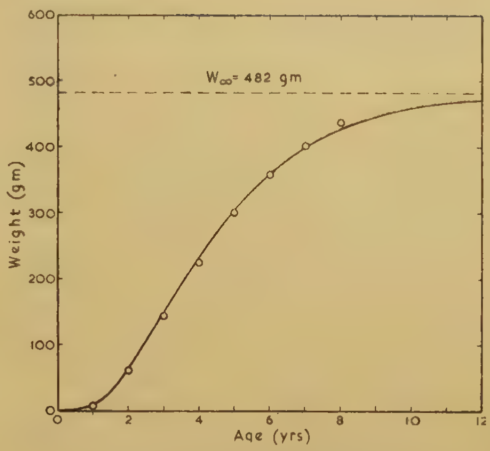

FIG. 16.10 GROWTH IN WEIGHT OF NORTH SEA SOLE

[Length data from Buckmann (1934) converted to weight and the fitted von Bertalanffy curve with parameter values $W_\infty = 482$ gm., $K = 0.42$, $t_0 = 0.3$ yrs.; from Table 16.7, columns C and D. This example is noteworthy in that nearly the whole of the growth pattern is covered by the data and fitted well by the von Bertalanffy equation.]

Buckmann showed that a cubic equation graduates the weight-length data satisfactorily, with

$$q = 0.009$$

Using this value to convert the observed lengths to weights gives the calculated figures of column C and an asymptotic weight of

$$W_\infty = 482 \text{ gm.}$$

The theoretical curve of growth in weight calculated with the above parameter values is shown in Fig. 16.10 together with the weights of column C, and the theoretical weight for each year of life is also tabulated in column D. Fig. 16.10 shows that nearly the whole of the growth pattern is covered by the data and that the von Bertalanffy equation gives a good fit over a wide range of weight; to this extent the sole therefore provides a better test of the applicability of the equation than do any of the previous examples.

Now the reason why the sole data cover such a wide range of the growth curve is not that the samples included older fish than in the cases we have discussed previously, but that the pattern of growth is effectively completed in a relatively shorter time. In other words, we might say that a sole of a given age is 'further developed' than a plaice, haddock or cod of the same age, in that a greater proportion of its growth pattern will have been completed when that age is reached. The concept of 'physiological age' has been developed in this connection, but this term does not seem to have been given a precise definition; some of the confusion that has been caused is discussed by Medawar (1945, p. 164), who concludes that it is possible to say only that one organism develops faster than another. We suggest that the 'rate of development' can be given a more precise and useful definition in terms of the rate at which the *growth pattern* is developed, and for a measure of this we can take the time required for a fish to reach a weight which is any specified proportion of the asymptotic weight W_∞. Suppose we let this weight be w_i and the proportion x, so that we can put

$$w_i = xW_\infty$$

and define by t_i the age at which the fish reaches this weight w_i. Now we can write

$$w_i = W_\infty\,(1 - e^{-K(t_i - t_0)})^3$$

and substituting for w_i in terms of W_∞ gives

$$t_i - t_0 = \frac{1}{K} \log\left(\frac{1}{1 - x^{1/3}}\right)$$

But x is an arbitrary constant and $t_i - t_0$ is the time taken to reach weight w_i from the 'true' origin, t_0, of the growth curve. Thus the rate at which the growth pattern is developed is found to be proportional to the coefficient of catabolism, K, and the value of K can be used as an index of what could be termed the 'intrinsic development rate' of the species. From the values of K for the four species considered above we can therefore say that a cod and haddock of the same actual age are also about the same 'physiological age' in that they have reached the same relative stage in the development of their growth pattern; but that a sole of this actual age would be more than twice, and a plaice about half, this physiological age. It will be noted that K can be regarded as independent of the level of feeding but might be expected to vary with certain environmental factors such as temperature. Thus, ultimately, we cannot interpret the growth of an organism except with reference to its particular environment.

In conclusion we would add that from an examination of the published growth data for a number of species of fish it would seem that the von Bertalanffy equation has a wide application. In most cases the fit to the data is as good, or nearly as good, as in the four species considered above, while in the remainder the departures are not greater than might be expected from sampling errors or biological factors such as a change in the type or consumption of food with increasing age.

16.3 WEIGHT DIFFERENCES BETWEEN INDIVIDUALS OF THE SAME AGE

On several occasions in previous sections we have had cause to refer to differences in weight of young plaice of the same age, and also the fact that recruitment occurs into four age-groups, indicating that some kind of weight threshold might operate. It was suggested that migration from the nursery grounds to the main exploited area might be conditioned largely by the size of the fish and its rate of growth, although we could not completely eliminate the influence of legal size limits in tending to impose an artificial threshold after recruitment has taken place. We now attempt to estimate the average weight of each recruit sub-group with certain alternative assumptions concerning its growth after recruitment (§16.3.1). In §16.3.2 we show that some discrimination between these hypotheses can be obtained by analysing the weight distributions at higher ages. The methods used do not depend on whether the 'weight threshold' is a natural or an artificial one.

16.3.1 *Formulation of three hypotheses concerning the relationship between pre- and post-recruit growth rates*

To establish the method we shall use the same terminology as in §15.1.3, and in addition denote by ${}_r w_{\theta_p + r}$ the mean weight at recruitment of fish of the sub-group r entering into age-group $\theta_p + r$, and by $\bar{w}_{\theta_p + r}$ the mean weight of all recruited fish of age-group $\theta_p + r$, including the sub-group ${}_r R$. Since θ_p is defined as the youngest age-group into which recruitment occurs, we have the identity

$$\bar{w}_{\theta_p} \equiv {}_0 w_{\theta_p}$$

being the average weight of fish of sub-group ${}_0 R_{\theta_p}$. Age-group $\theta_p + 1$ contains recruits into sub-group ${}_1 R$ of mean weight ${}_1 w_{\theta_p + 1}$, and ${}_0 R_{\theta_p + 1}$ survivors from sub-group ${}_0 R_{\theta_p}$ which now weigh ${}_0 w_{\theta_p + 1}$. These are, of course, indistinguishable in samples but the average weight of all fish of age-group $\theta_p + 1$ in samples is

$$\bar{w}_{\theta_p + 1} = \frac{{}_0(wR)_{\theta_p + 1} + {}_1(wR)_{\theta_p + 1}}{{}_0 R_{\theta_p + 1} + {}_1 R_{\theta_p + 1}}$$

so that the average weight of fish of sub-group ${}_1R$ is

$$ {}_1w_{\theta_p+1} = \frac{\bar{w}_{\theta_p+1}\left({}_0R_{\theta_p+1} + {}_1R_{\theta_p+1}\right) - {}_0(wR)_{\theta_p+1}}{{}_1R_{\theta_p+1}} $$

It will be seen that this procedure can readily be generalised to give the average weight of recruits in sub-group ${}_rR$ as

$$ {}_rw_{\theta_p+r} = \frac{\bar{w}_{\theta_p+r} \sum_{z=0}^{r} {}_zR_{\theta_p+r} - \sum_{z=0}^{r-1} {}_z(wR)_{\theta_p+r}}{{}_rR_{\theta_p+r}} \quad \ldots \quad \ldots \quad \ldots \quad (16.5) $$

(cf. (15.12))

the second summation term being disregarded for $r = 0$.

The first requirements for application of (16.5) to plaice are estimates of $\bar{w}_{\theta_p+r}$, i.e. the average weight of each age-group at the recruitment season. Sampling was not continuous then, but satisfactory estimates can be obtained by using the average weights in samples taken at Lowestoft in October during the years 1929-38, which are entered in column B of Table 16.8. The values of ${}_rR_{\theta_p+r}$ as indices of abundance, i.e. the catch per 100 hrs. of recruits into each age-group, have been given in row D of Table 15.6. As in §15.1.3 we shall assume that all fish when recruited are subject to the same mortality, of which we use the estimate $(F + M) = 0.83$ (see §13.2), this mortality becoming effective at the values of ${}_rt_p$ given on page 260. For example, the relative number of fish in sub-group ${}_0R$ which survive to age ${}_rt_p$, i.e. the age at which the sub-group ${}_rR$ is recruited, is

$$ {}_0R_{\theta_p+r} = {}_0Re^{-(F+M)({}_rt_p - {}_0t_p)} $$

$$ = 639 \times e^{-0.83({}_rt_p - {}_0t_p)} \quad \ldots \quad \ldots \quad \ldots \quad (16.6) $$

The procedure for determining sub-group numbers is fairly clear, but the difficulty arises in specifying the growth rate of each sub-group after it has entered the exploited area; in the case of sub-group ${}_0R$, for example, we shall know ${}_0w_{\theta_p}$ but must suggest hypotheses for predicting subsequent values ${}_0w_{\theta_p+1}$, ${}_0w_{\theta_p+2}$, etc. . . . . . . ${}_0w_{\theta_p+r}$. The simplest (*hypothesis* (*j*)) would seem to be that the mean growth of each sub-group after recruitment can be described by the same values of W_∞ and K, these being the average values for the whole post-recruit phase already determined in §16.2.1, viz.: 2867 gm. and 0.095 respectively. The mean rate of increase of weight with age would then be different for each sub-group, but only by virtue of their differing weights at recruitment; differences in growth pattern would be assumed to be confined to the pre-recruit phase. An approximation to such a situation might arise if differences in the intrinsic growth potential among individuals (i.e. in the value of K) were small, and competition for food was intense only in the pre-recruit phase. More usually, however, we should expect to find that certain members of a year-class possessed physiological characteristics that enabled them in any case to grow faster than others (as is, in fact, shown by Dawes' (1930, 1931) experiments on growth of plaice discussed in §16.4.2.3), and that these characteristics persisted, to a greater or lesser extent, throughout life. Whether or not the fish with the favourable metabolic characteristics (i.e. high values of E and K) are, for this reason alone, able to reach and consume more food, there are nevertheless likely to be differences in the food consumption of fish which are to be expressed in terms of differences in W_∞. While we cannot deduce from general considerations alone the relative variations in these two parameters which will occur, we can obtain some appreciation of the problem by taking two extreme hypotheses; *hypothesis* (*k*), in which the whole of the differences in pre-recruit growth are represented in terms of changes in W_∞, and *hypothesis* (*l*), in which these differences are represented by appropriate differences in K. In each case we shall assume that these differences persist throughout life, and that the parameter remaining constant has the average value found previously, i.e. $W_\infty = 2867$ gm., $K = 0.095$.

We now have sufficient information to use (16.5) to compute the average weight of fish in each recruit sub-group according to the three hypotheses defined above. The calculation is carried out with r having the value 0, 1, 2 and 3 in turn, and with $\theta_p = 2$. For example, the average weight of group-II fish in the samples is ${}_0w_{\theta_p} = 151$ gm., which is also the average weight of fish in sub-group ${}_0R$ [i.e. $r = o$ in (16.5)]. This quantity is therefore the first entry in columns B, C, D and E of Table 16.8. The number surviving to the following recruitment season is found from (16.6) to be 303, using the estimates of the mean age at recruitment ${}_1t_p = 3.35$ years and ${}_0t_p = 2.45$ years given on p. 260. The weight of those fish according to hypothesis (j) is given by

$${}_0w_{\theta_p+1} = \{W_\infty^{1/3} - (W_\infty^{1/3} - {}_0w_{\theta_p}^{1/3})\, e^{-K({}_1t_p - {}_0t_p)}\}^3$$

in which $W_\infty = 2867$ gm., $K = 0.095$ and ${}_0w_{\theta_p} = 151$ gm., and is found to be 221 gm. From hypothesis (k) however, a weight of 151 gm. at 2.45 years may be obtained by a value of ${}_0W_\infty$ given by

$${}_0W_\infty = \frac{{}_0w_{\theta_p}}{(1 - e^{-K({}_0t_p - t_0)})^3}$$

in which $K = 0.095$ as before. In this way ${}_0W_\infty$ is found to be 7921 gm. entered in column F, and with this value these fish will reach a weight at the next recruitment season of

$$\begin{aligned}{}_0w_{\theta_p+1} &= \{7921^{1/3} - (7921^{1/3} - 151^{1/3})\, e^{-0.095 \times 0.9}\}^3 \\ &= 277 \text{ gm.}\end{aligned}$$

From hypothesis (l) we have

$${}_0K = \frac{1}{t_0 - {}_0t_p} \log \left\{1 - \left(\frac{{}_0w_{\theta_p}}{W_\infty}\right)^{1/3}\right\}$$

in which $W_\infty = 2867$ gm. Inserting the same estimates for ${}_0w_{\theta_p}$ and ${}_0t_p$ as before gives ${}_0K = 0.144$ entered in column G. Thus with hypothesis (l) the average weight of fish of sub-group ${}_0R$ at the following recruitment season is

$$\begin{aligned}{}_0w_{\theta_p+1} &= \{2867^{1/3} - (2867^{1/3} - 151^{1/3})\, e^{-0.144 \times 0.9}\}^3 \\ &= 262 \text{ gm.}\end{aligned}$$

Proceeding in this way we estimate the recruitment weight of each sub-group according to the three above hypotheses (columns C, D and E), the appropriate values of ${}_rW_\infty$ and ${}_rK$ for hypotheses (k) and (l) being given in columns F and G. It will be noticed that the weights in each of columns C, D and E vary less within a column than those in column B, so that whichever hypothesis is used to predict the subsequent growth of each recruit sub-group, the result appears to confirm the existence of a weight-threshold for recruitment. However, with hypotheses (k) and (l) the average weight of group-V recruits is lower than that of any other sub-group; this may be real, but it is more likely that these hypotheses predict a rather too rapid post-recruit growth for the younger sub-groups, which would have the same effect on the predicted weight of group-V recruits.

16.3.2 *Some implications of these hypotheses*

With hypotheses (k) and (l) it is assumed that the mean growth of each recruit sub-group can be described throughout life by a particular value of W_∞ or K respectively.

Consequently, each hypothesis implies a certain distribution of one or other parameter among a fully recruited year-class, and one requirement of these predicted distributions is that they should have the same mean values as those found in §16.2 for the post-recruit phase.

The number in the rth recruit sub-group in the first fully recruited year-class is given by the expression

$$_rRe^{-(F+M)({}_{\Phi}t_\rho - {}_rt_\rho)}$$

where Φ is the total number of sub-groups and ${}_{\Phi}t_\rho$ is the date on which the oldest of these is recruited. With values of ${}_rR$ taken from row D of Table 15.6, recruit sub-groups are found to be represented in a fully recruited year-class in the proportions

$$0.0267 : 0.2685 : 0.5346 : 0.1702$$

These can be used as weighting factors to compute a mean value of W_∞ or K for the whole year-class. Thus, with hypothesis (k) and using estimates of ${}_rW_\infty$ for each sub-group given in column F of Table 16.8, we find $\bar{W}_\infty = 3102$ gm. Similarly, for hypothesis (l), we have $\bar{K} = 0.098$. Both these values are slightly higher than those found in §16.2 but the agreement is nevertheless good and it can be concluded that neither hypothesis (k) nor (l) is in this respect inconsistent with the observed average growth of an entire year-class.

Another approach which can throw some light on the subsequent growth of each recruit sub-group is to compare the average weight of fish in fully recruited age-groups predicted by each of the above hypotheses with that observed in market samples. We first need to calculate the average weights attained by each recruit sub-group at any given later age; with hypothesis (j), the weight of fish of the sub-group r when in the θth age-group can be written as

$${}_rw_\theta = \{W_\infty^{1/3} - (W_\infty^{1/3} - {}_rw_{\theta_\rho + r}^{1/3})\, e^{-K(\theta - {}_rt_\rho)}\}^3 \quad .. \quad .. \quad .. \quad (16.7)$$

where $W_\infty = 2867$ gm. and $K = 0.095$. For the sub-group ${}_0R$ at age 5.7 years for example (i.e. $\theta_\rho = 2$, ${}_0t_\rho = 2.45$, $r = 0$), (16.7) using hypothesis (j) gives a weight of 452 gm.; putting $r = 1$, 2 and 3 successively, gives the weights of the other sub-groups at this age as 373 gm., 294 gm. and 200 gm. respectively. These four sub-groups comprise the whole year-class at this and higher ages, and are present in the proportions given above; using these as weighting factors as before, the average weight of all V-group fish is found to be $\bar{w}_V = 303$ gm., being the first entry in column B of Table 16.9. The mean weight of age-groups VI to X computed in this way are the remaining entries in column B. Columns C and D give the mean weights predicted by hypotheses (k) and (l); these are computed similarly, except that the appropriate value of ${}_rW_\infty$ or ${}_rK$ for each sub-group (columns F and G of Table 16.8) are used in (16.7). The observed mean weights for age-groups V to X are shown in column E, these being taken from the bottom row of Table 16.2. Comparison of predicted and observed mean weights shows that the former for all hypotheses are higher than the latter, although the differences are not great. Hypothesis (j) gives estimates about 4-5% higher than the observed values, while the difference in the case of hypothesis (l) is about 7% and with hypothesis (k) about 10%. This result for the last two hypotheses is in accordance with our previous finding that the mean W_∞ and K predicted by them are a little greater than those determined in §16.2.1.

A more critical test of the three hypotheses would be to compare the weight dispersion predicted by them in fully-recruited age-groups with that observed in samples. The difficulty here is that we are unable to observe directly the weight dispersion *within* each recruit sub-group; in the foregoing we have, in fact, dealt only with the mean growth of each. If, however, we predict dispersions on the assumption that all individuals of each sub-group are the same weight, the observed dispersions should be greater because they include the dispersion within each sub-group. The predicted weight dispersion in age-groups V to X can be calculated according to each hypothesis from the mean weights of each sub-group that have already been used to compute the mean weight of fully-recruited age-groups given in Table 16.9, using the same weighting coefficients as before. As an index of dispersion we use the standard deviation, and values of this predicted by each hypothesis are given in columns G, H and J of Table 16.9. It was not possible in preparing this paper to estimate weight dispersions for pre-war data, but since we have no reason to believe that these had changed appreciably we have used the market sample data obtained in 1948. The mean weights of fish in age-groups V to X in these samples are given in column F; these are a little greater than the pre-war estimates for most age-groups, but because of this they are very similar to the predicted mean weights, so that a direct comparison of standard deviations is facilitated. Observed values of σ are given in column K, and a better discrimination between the three hypotheses can now be obtained by plotting σ against age as shown in Fig. 16.11. It is now clear that hypothesis (j) is unacceptable, since the differences between columns G and K are too great to be ascribed to dispersion within each sub-group. On the other hand, values of σ predicted by hypothesis (k) are nearly all a little greater than the observed values, even although they do not include sub-group weight dispersion; this indicates that to ascribe weight differences at recruitment entirely to differences in W_∞ that are maintained throughout life is probably too extreme.

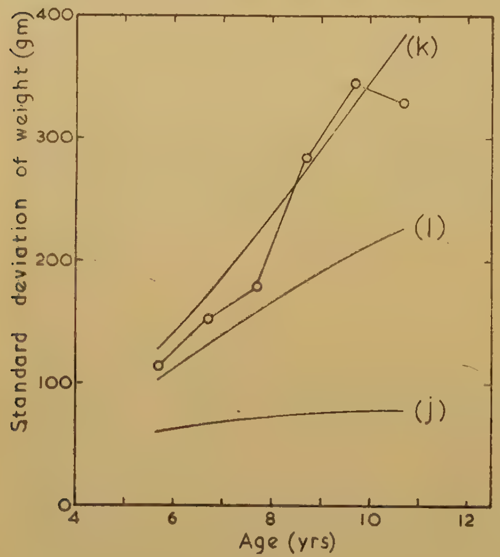

FIG. 16.11 WEIGHT DISPERSION IN PLAICE
[Predicted and observed standard deviations of weight among fish of certain age-groups; from Table 16.9, columns G, H, J and K.]

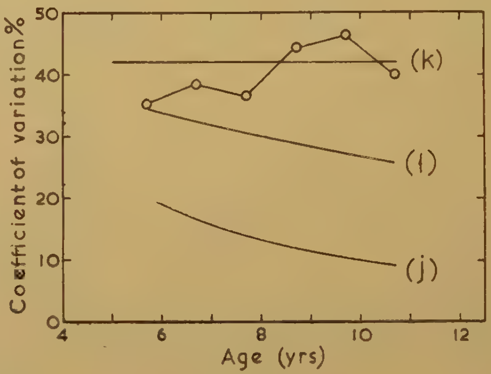

FIG. 16.12 WEIGHT DISPERSION IN PLAICE
[Predicted and observed coefficients of variation of weight among fish of certain age-groups; from Table 16.9, columns L, M, N and P.]

Another way of comparing the predicted and observed weight dispersions is to compute the coefficient of variation of weight at each age for each hypothesis. These are entered in columns L, M and N of Table 16.9, together with observed coefficients in column P. These data are plotted in Fig. 16.12, and it is seen that whereas hypotheses (j) and (l) imply a continual decrease with age, hypothesis (k) gives a constant value. The observed coefficients show no tendency to decrease with age—if anything, the reverse—which suggests that although hypothesis (k) predicts rather too great dispersion, it nevertheless results in a dispersion pattern that changes with age in a way most similar to what is observed.

In conclusion, it should be stressed again that this investigation does not attempt to deal with the growth history of individual fish, but is concerned with working out the consequences of certain assumptions about the mean growth in each recruit sub-group after it has been recruited. It does not prove directly whether the identity—in terms of growth characteristics—of a sub-group is retained after recruitment, and it is theoretically possible for the observed differences in weight between individuals of a fully recruited year-class to be caused by transitory changes in growth rate unrelated to their growth characteristics as pre-recruits. Some variation is undoubtedly of this kind, but the observed weight differences are so great that it is difficult to accept this as a sufficient explanation, especially as large intrinsic differences in growth potential between individual fish have been demonstrated experimentally (see §16.4.2). Some discrimination between these two causes of weight dispersion might come from a study of otolith structure; here it is sufficient to note that whatever the true mechanism, assuming the growth of each recruit sub-group to be defined by a particular value of W_∞ retained throughout life (hypothesis (k)) produces a pattern of weight dispersion among older fish that agrees best with data, although the extent of that dispersion is almost certainly exaggerated. Incorporating hypothesis (k) into theoretical models therefore enables some idea to be obtained of the maximum effect that could result from weight dispersion in plaice, as is discussed further in §18.3.1.

16.4 DEPENDENCE OF GROWTH ON POPULATION DENSITY, FOOD AVAILABILITY AND FOOD CONSUMPTION

16.4.1 *Empirical relationships between growth and population density*

As mentioned in §9.4.2, there are two main types of situation which can provide information concerning the relationship between the density of a population and the growth of individuals comprising it. The first arises when two or more levels of density have existed, each lasting a sufficient time for the population of fish in question and those of the food organisms to have reached stability, an approximation to which case is provided by the plaice (§16.4.1.1). This situation enables a direct estimate of the required relationship to be made—one which is suitable for use in population models to predict the steady state of a population corresponding to any desired level of fishing intensity or mesh size. The other type of situation is that in which transitory fluctuations in density have occurred which may be correlated with the corresponding growth. To predict the equilibrium relationship between density and growth from observations of this latter kind, when neither the fish nor the food populations are stable, is more complex. In §16.4.1.2 we discuss a method for analysis of this kind of data, using as an example the North Sea haddock, in which the variations in density are due primarily to fluctuations in annual recruit numbers.

16.4.1.1 *Plaice—the analysis of two steady states*

We have attempted to relate annual fluctuations in growth of plaice during the periods 1929-38 and 1946-48 to estimates of both the corresponding number-density and the biomass of the population, the latter being obtained from age-compositions and commercial statistics of catch per unit effort. No correlation was detectable in the pre-war series of data, largely because variation in population density was slight. It will be remembered that a similar difficulty was experienced in §14.3.2.2, when attempting to determine the natural mortality of plaice by analysis of year-to-year fluctuations in total mortality and fishing intensity.

The year 1946-47 might have been expected to have given a more conclusive result, since the average density at this time was about twice as high as the pre-war level. This was not the case, however, and the 1946-47 growth was only a little lower than the pre-war average, and certainly did not differ significantly from it. It might be inferred from this that the dependence of growth on population density in the plaice population under investigation is not likely to be particularly pronounced. This was confirmed when the second approach mentioned above was adopted and the growth during the whole of the war period, during most of which time the density was high, was compared with the pre-war growth: this showed, nevertheless, that a definite effect of density on growth does exist.

Those year-classes fully represented in the catch before the war, and yet sufficiently abundant in 1946 to be sampled adequately, are those which formed the X to XIII age-groups in that year, i.e. the 1933-36 year-classes. Their average weights during 1946 are shown in column E of Table 16.10. The weights of these year-classes during 1938 were very near to the average values for that age, but tending, if anything, to be slightly higher.

From the discussion in §9.4.1 it will be remembered that there are reasons to believe that variations in growth rate due to changes in food supply (which we are taking to be the main effect of a change in population density) are best represented in the von Bertalanffy equation by differences in the value of the growth parameter W_∞ (or L_∞). Since we have no data referring to the complete year 1939, we have used the theoretical weights at ages 3.7, 4.7, 5.7 and 6.7 years (column B) to compute estimates of the average W_∞ over the seven-year war-period, using the particular form of the von Bertalanffy equation

$$W_\infty^{1/3} = \frac{w_{t+7}^{1/3} - w_t^{1/3} e^{-7K}}{1 - e^{-7K}}$$

The resulting values are given in column F. Similar estimates relating to the growth between the same ages over the period 1929-38 of the 1922-28 year-classes are given in columns J, M, P and S. We have therefore a mean estimate of W_∞ for each of two periods, namely

$$\text{a pre-war mean of } W_\infty = 3150 \text{ gm.}$$

and

$$\text{a war-time mean of } W_\infty = 2177 \text{ gm.}$$

Inspection of Table 16.10 shows that the war-time W_∞ is lower than any of the pre-war values, and a t-test showed that the difference was highly significant. It will be noted that the estimate given above of the pre-war W_∞ is a little higher than the value derived in §16.2.1. This is due to the fact that it was computed in a rather different way, and refers to a limited range of ages only. A fair estimate of the war-time W_∞, to be compared with the pre-war value of 2867 gm., is probably

$$\frac{2177 \times 2867}{3150} = 1982 \text{ gm.}$$

Since there was no sampling during the war, we do not know directly the changes in density which resulted from the cessation of fishing, but a comparison of the immediate pre- and post-war densities from data given by Margetts and Holt (1948, Table 20) suggests that the average war-time biomass was at least three times the pre-war level. With only two values of density and corresponding asymptotic weights, we first tried a linear relationship of the form

$$W_\infty = a + bR\left(\frac{\bar{P}_W}{R}\right)$$

but this gave negative values of W_∞ at the high densities associated with very low fishing mortalities, and it seemed that a curve was required in which W_∞ approached zero more slowly with increases in density. We have therefore related to biomass by a linear equation the values of L_∞ corresponding to those of W_∞ given above (implying a cubic relationship between W_∞ and biomass).* Thus in the equation

$$L_\infty = a + bR\left(\frac{\bar{P}_W}{R}\right)$$

we have

$$\text{pre-war } L_\infty = 68.5 \text{ cm. (see § 16.2.1)}$$

and

$$\text{war-time } L_\infty = \sqrt[3]{\frac{1982}{0.00892}} = 60.57 \text{ cm.}$$

---

*An analytical treatment of interaction between a fish population and its food, the results of which are presented in §18.4.2.6, showed that this procedure probably gives a satisfactory representation of the relation between growth and biomass over a fairly wide range.

In addition, the theoretical value of $\bar{P}_W/R$ for plaice corresponding to the mean pre-war fishing mortality coefficient of $F = 0.73$, is found from Table 17.1 and Fig. 17.3 to be

$$\frac{\bar{P}_W}{R} = 266.34 \text{ gm.}$$

Thus we have the simultaneous equations

$$68.5 = a + bR \times 266.34$$

$$\text{and } 60.57 = a + 3bR \times 266.34$$

giving the values

$$a = 72.47 \text{ cm. (equivalent to 3395 gm.)}$$

$$\text{and } bR = -0.0149$$

which we have used in the calculations of Part IV.

It should be mentioned that the majority of plaice of the high ages which we have had to use to obtain these estimates were females, but although the proportion of males had increased to some extent by the end of the war, this had no serious effect on the comparative value of the average weights in 1946 of the age-groups in question. The number of males in the samples of these age-groups was insufficient to permit an independent estimate of the change in their growth rate to be made, but there is no reason to believe that increases in population density would have resulted in greatly differing effects on the growth pattern of the two sexes.

16.4.1.2 *Haddock—the analysis of fluctuations*

We now proceed to a discussion of the use of fluctuating data to predict an equilibrium relationship between growth and population density. Since we shall be exemplifying these methods with pre-war haddock figures published by Raitt (1939), which consist of length measurements and estimates of annual mean population numbers, it is convenient to refer to these particular quantities in what follows, but it will be seen that the methods are equally applicable to data of weight and biomass.

A satisfactory index of yearly growth can be obtained by representing variations in growth by appropriate changes in L_∞. Thus we may write (3.8) in the form

$$ {}_{\theta}(L_\infty)_X = \frac{{}_{\theta+1}(l)_{X+1} - {}_{\theta}(l)_X e^{-K}}{1 - e^{-K}} \qquad .. \qquad .. \qquad (16.8)$$

where ${}_{\theta}(l)_X$ and ${}_{\theta+1}(l)_{X+1}$ are the lengths of a fish at ages θ and $\theta + 1$ at the beginning of the years X and $X + 1$ respectively, and K is constant. The quantity ${}_{\theta}(L_\infty)_X$ is thus the value of the parameter L_∞ describing the growth of age-group θ in year X, and it will be seen to take into account both the size of fish at the beginning of the year in question and also the growth increment during that year. There are, however, two ways in which estimates of relation between growth and density obtained from a fluctuating series of data may differ from the equilibrium relation, the first being due primarily to the behaviour of the food population and the second to that of the fish themselves.

Suppose we have a number of observed values of annual population numbers which form a fluctuating series in time, each of these values being associated with a value of L_∞ for that year which we shall distinguish from the true equilibrium value corresponding to the value of $\bar{P}_N$ in question by writing as $(L_\infty)'$. We may therefore denote by $(\bar{P}_N)_X$ and $(L_\infty)'_X$ respectively the values of these two quantities in any given year X. In the first place we suppose that the food available to the population at the beginning of year X is independent of the density of the population in previous years, i.e. of $(\bar{P}_N)_{X-1}$, $(\bar{P}_N)_{X-2}$, etc., which would be the case if the life-span of the food species were a single year only (i.e. $\lambda' = 1$).* Then $(\bar{P}_N)_X$ and $(L_\infty)'_X$ would have their true equilibrium relationship, and the series of data could be analysed as if each year referred to an equilibrium level of population density. If, however, the life-span of the food species is longer than a year, we may put

$$\lambda' \simeq 1 + \theta'$$

where θ' is an integer. The food available at the beginning of year X will now depend on the θ' preceding values of $\bar{P}_N$, i.e. the series $(\bar{P}_N)_{X-1}$, $(\bar{P}_N)_{X-2}, \ldots$ etc.$\ldots(\bar{P}_N)_{X-\theta'}$, and we may proceed as follows.

Let us suppose, for simplicity, that an equilibrium relationship between L_∞ and $\bar{P}_N$ can be represented by the linear equation

$$L_\infty = a + b\bar{P}_N \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (16.9)$$

Then if we have a series of yearly values, $(L_\infty)'_X$ and $(\bar{P}_N)_X$, they will be related by the equation

$$(L_\infty)'_X = a + b_0(\bar{P}_N)_X + b_1(\bar{P}_N)_{X-1} + \ldots + b_r(\bar{P}_N)_{X-r} + \ldots + b_{\theta'}(\bar{P}_N)_{X-\theta'} \ldots \quad (16.10)$$

The coefficients b_r denote the effect of the density $(\bar{P}_N)_{X-r}$ in year $X - r$ on the growth in year X, and are such that

$$\sum_{r=0}^{\theta'} b_r = b \text{ (of (16.9))} \quad \ldots \quad \ldots \quad \ldots \quad (16.11)$$

In the steady state we shall have

$$(\bar{P}_N)_X = (\bar{P}_N)_{X-1} = (\bar{P}_N)_{X-r} = (\bar{P}_N)_{X-\theta'}$$

in which case (16.10) is identical to (16.9), as required. The coefficients a and b of (16.10) can be determined from data by a multiple regression analysis (see, e.g. Kendall (1948)), the principle of which is to minimise the sums of the quantities

$$\{(L_\infty)'_X - (a + b_0(\bar{P}_N)_X + \ldots + b_{\theta'}(\bar{P}_N)_{X-\theta'})\}^2$$

Values of the coefficients b_r should decrease as r increases, in theory becoming zero when

$$\theta' > \lambda' - 1$$

For practical purposes the series would be terminated at a value of θ' such that $b_{\theta'+1}$ did not differ significantly from zero. The required value of b of (16.9) referring to the steady state would then be obtained from (16.11). It will be seen that if we were to fit the simple regression (16.9) without taking account of the preceding values of $\bar{P}_N$, we should obtain an estimate of the coefficient b_0' of the equation

$$(L_\infty)'_X = a + b'_0(\bar{P}_N)_X \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (16.12)$$

Now, if successive densities $(\bar{P}_N)_X$, $(\bar{P}_N)_{X-1}\ldots$etc., are independent, then

$$b'_0 = b_0 = b - \sum_{r=1}^{\theta'} b_r < b$$

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*Strictly, independence of this kind requires also that the recruitment to the food population be uncorrelated with the abundance of the mature individuals comprising it in previous years, at least, within the range of abundance concerned. In the absence of any indications to the contrary, however, we assume in the following analysis that this requirement is satisfied.

so that b_0' will be lower than the true value b to an extent depending on the sum of the subsequent coefficients b_r. If, however, successive densities are not independent, the value of b_0' will increase by an amount depending on the correlation between them, but only in the special case of

$$(\bar{P}_N)_X = (\bar{P}_N)_{X-1} = \text{etc.},$$

will $b_0' = b$. In practice, (16.12) will therefore always give an underestimate of the true effect of density on growth, and as we shall show in §18.4, this is more serious when assessments of the probable effects of regulative measures are being made than if the effect is overestimated.

The second factor tending to distort the picture when an attempt is made to determine parameters for the steady state from fluctuating data is that whether variation in the values of $\bar{P}_N$ is due to fluctuations in annual recruitment or fishing mortality, high values of $\bar{P}_N$ will tend to be associated with a mean population age less than that for the steady state corresponding to that value of $\bar{P}_N$, and *vice-versa*. Consequently the size distribution of fish would not be the same in the two cases, but the effect of this on the estimate of the relationship between L_∞ and $\bar{P}_N$ depends on a number of factors and cannot be assessed without an analytical treatment taking into account factors such as the food requirements of fish of different sizes (see §§9.4.3 and 18.4.2.6).

We now consider the pre-war haddock data, in which Raitt himself detected a relationship between growth and density. Thus he found that the average lengths of some year-classes were inversely related to their abundance, though there were certain exceptions to this rule which he explained by referring to competition between year-classes. Our conclusions agree with Raitt's finding of a relationship between growth and density, and we have found that use of the von Bertalanffy equation to provide indices of yearly growth permits a fuller interpretation of the data.

Raitt (1939, Table 7) gives the average length reached by a number of year-classes at the end of their second, third and fourth years of life, for each of the growth areas distinguished by H. Thompson (1929) and referred to by him as the Eastern, Western and Central areas. We have calculated values of L_∞ describing the growth of those year-classes during the years 1927-37 by means of (16.8), using the value $K = 0.2$ found in §16.2.2, and they are tabulated in columns C, D and E of Table 16.11. For example, the average length of fish of the 1926 year-class in the Western area at the end of their first year of life was 16.7 cm. and at the end of their second year, 24.8 cm. Thus our index of the growth of the I-group fish during 1927 is given by

$${}_{\text{I}}(L_\infty)_{1927} = \frac{24.8 - 16.7\,e^{-0.2}}{1 - e^{-0.2}} = 61.4 \text{ cm.}$$

which is the first entry of column C. A simple index of density in each area, obtainable directly from the data presented by Raitt (Tables 3 and 4), is the combined numerical abundance of all age-groups from I-VI. These are given in column F of Table 16.11 as the catch in numbers per 1/100 hr. fishing by the research vessel EXPLORER; they are therefore only indices of the true population numbers $\bar{P}_N$, and for the moment we shall denote them by $\bar{N}$. In Fig. 16.13 are shown the values of L_∞ for each age-group in each area plotted against the corresponding density index of column F, with the least squares regression lines for the Western and Central areas. In these two areas the relationship is well represented by straight lines with negative slopes, but this is not so in the Eastern area for which the regressions do not depart significantly from the horizontal. It may be noted here that postulating a linear relationship between L_∞ and number-density is in harmony with the results of an analytical treatment of a fish population and its food as a predator-prey system, described in §18.4.2.6. It is shown there that population number is possibly a rather better index of density to relate linearly to L_∞ than is biomass, although the indications are that either is satisfactory for most purposes.

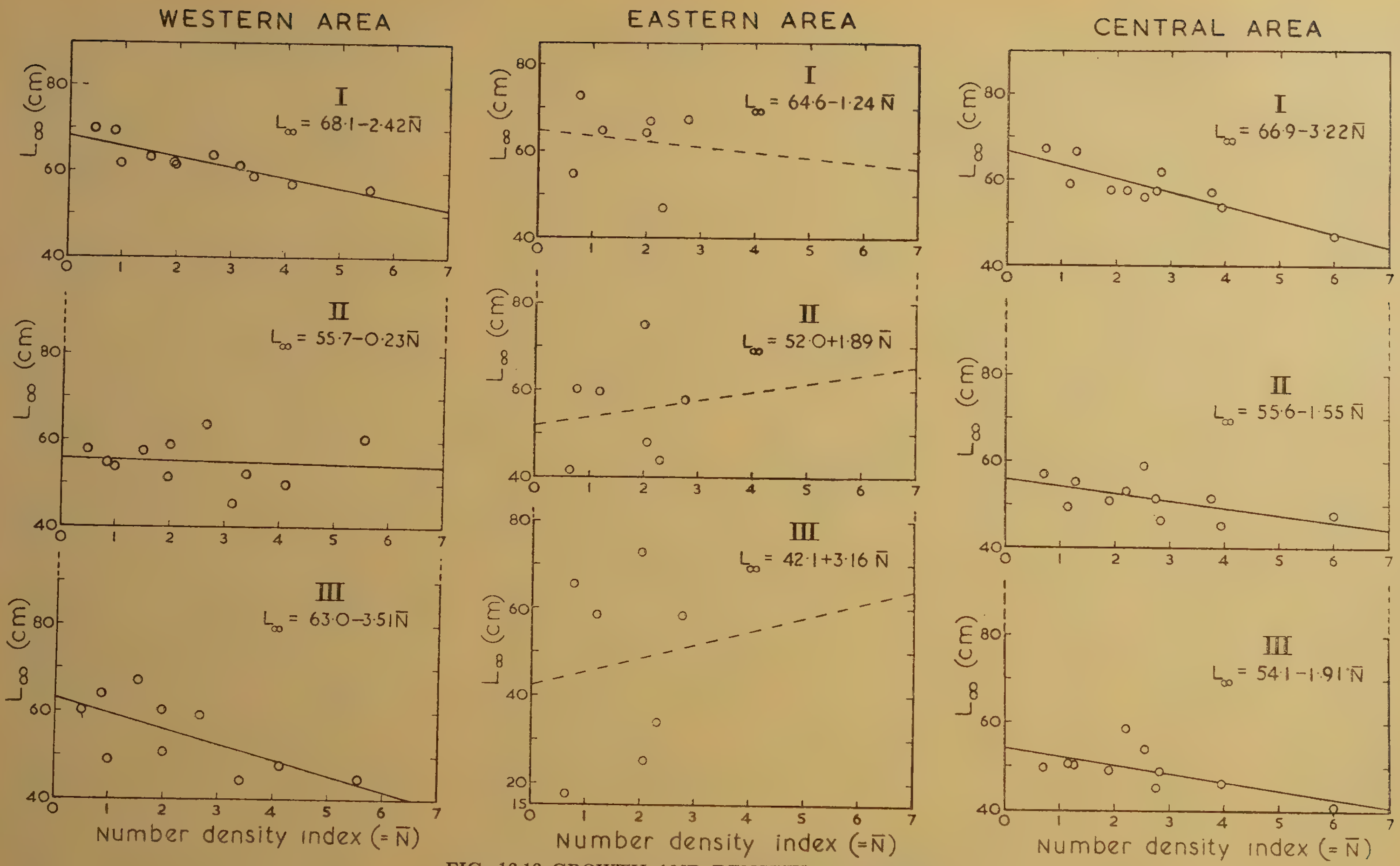

FIG. 16.13 GROWTH AND DENSITY IN HADDOCK

[Estimates of L_∞ for age-groups I, II and III in the three growth areas distinguished by H. Thompson (1929) plotted against indices of density ($\bar{N}$) of age-groups I to IV; from Table 16.11.]

The pioneer work of Thompson (*ibid*) on the North Sea haddock established that there are differences in the rate of growth in the three areas referred to above, it being highest in the Eastern area and lowest in the Central, with the Western area intermediate. With our methods these differences should be apparent in the mean values of L_∞ for each area, and from Table 16.11 this is seen to be the case as far as the Central area having the lowest rate of growth is concerned; the Eastern and Western areas appear to have about the same rate of growth, but the variation of L_∞ in the former is too great to allow any worthwhile comparison to be made.

Now it is also seen from Table 16.11 that the mean densities in each area are in an order opposite to that of the values of L_∞, and the question therefore arises whether these differences in density are sufficient in themselves to account for the differences between the rates of growth. An indication of whether this is the case can be obtained by determining the constants of the linear equation relating the mean L_∞ and the mean $\bar{P}_N$ for the Western and Central areas, since if the growth differences in the two areas are caused only by the differences in density, these constants should be approximately equal to the mean of those for the individual age-groups in the separate areas. From Table 16.11 we find

$$57.4 = a + 2.417\,b \text{ (Western area)}$$

$$53.0 = a + 2.644\,b \text{ (Central area)}$$

from which

$$a = 104.3 \text{ cm.}$$

and

$$b = -\,19.4$$

Both these constants are greater than any of those shown in Fig. 16.13 for the individual age-groups in either area, suggesting that there may be an intrinsic difference in growth rate between the Western and Central areas over and above that which would be expected as a result of the difference in the mean densities. We could not, of course, by this method distinguish between differences due to inherent differences between the growth potentialities of the fish themselves and those due to factors of the environment, such as food supply.

So far it has not been necessary to take account of the possibility that the growth in any one year may be influenced by the densities in preceding years, but we must now see whether this effect is important. We consider first the data for age-group I in the Western area, which it will be seen from Fig. 16.13 have the least scatter. Fitting and testing a multiple regression showed that the coefficients from b_2 onwards do not depart significantly from zero, but the first two coefficients are

$$b_0 = -\,2.347$$

$$b_1 = -\,0.963$$

of which the value of b_0 is highly significant ($p < 0.1\%$), as might be expected from the close fit of the regression, while that of b_1 is significant at about the 5% level. The value of b of the simple regression shown in Fig. 16.13* is $-\,2.422$, and for these data we may reasonably conclude that about a quarter of the effect of density on the growth of these fish in a given year is due to the density in the previous year. The effective life-span of the food species eaten by group I fish in the Western area therefore appears to be between one and two years (see §9.4.3.2.3).

When investigating in §18.4 the behaviour of population models containing growth-density relationships we did not attempt to consider regional differences in growth of haddock, since this would require a knowledge of the rate of interchange between the various growth areas and of the distribution of fishing effort, which is not available to us. In these circumstances the general relationship between growth and density in the haddock which we require is that obtained by combining all the data of Table 16.11. This procedure does not give such a good correlation as those for individual age-groups and areas, but this cannot be avoided. Thus fitting a multiple regression to the combined data gives a value of b_1 which does not differ significantly from zero, but the most probable estimate of b is not to be obtained from (16.11) using values of b_r which are not significant, since as r increases the available degrees of freedom become fewer and values of b_r can show wide variation. For later use we shall therefore take the simple regression based on the combined data of Table 16.11, which is

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*The value of the coefficient b for the simple regression is not the same as that for the multiple regression, but this is due to the fact that both regressions pass through the mean value of $\bar{N}$.

$$L_\infty = 59.28 - 1.758\bar{N}$$

It remains to relate the constants 59.28 and 1.758 found above to the parameters a and bR respectively in the equation

$$L_\infty = a + bR\left(\frac{\bar{P}_N}{R}\right)$$

The mean L_∞ from all the data of Table 16.11 is found to be 55.24 cm., which is slightly higher than the value 53 cm. obtained in §16.2.2. For our estimate of the constant a we have therefore taken the value

$$a = \frac{59.28 \times 53}{55.24} = 56.88 \text{ cm.}$$

The mean density index from Table 16.11 is 2.297, and it refers to the abundance of age-groups I to VI inclusive. The corresponding value of $\bar{P}_N/R$ is therefore given by (5.5) with $t_\lambda = 7$ years and with the parameter values determined in previous sections for the pre-war period, viz.: $F = 1.0$, $M = 0.2$ and $t_\rho = 1$ year. We shall take the pre-war cod-end mesh size as 70 mm., so that $t_{\rho'} = 1.83$ years. Thus we find

$$\frac{\bar{P}_N}{R} = 1.470$$

and hence

$$bR = -\frac{1.758 \times 2.297 \times 53}{1.470 \times 55.24}$$

$$= -2.636$$

16.4.2 *The dependence of growth on food consumption*

The utilisation of food by plaice for growth and maintenance has been studied only by Dawes (1930, 1931), and his experimental design has certain limitations for use in the present connection. Apart from the fact that the technique of measuring food consumption had not been perfected, experiments were based on very small numbers of young fish, and the annual cycle of growth was not completely covered. In addition, only one type of food was used, *Mytilus edulis*, which is not a natural food of plaice in the North Sea. Nevertheless, the results obtained by Dawes can give a provisional assessment of the effect of a change in the amount of food consumed by an individual fish on its rate of growth.

It is convenient to consider this problem in three stages, dealing firstly with maintenance requirements (§16.4.2.1), secondly with the efficiency of utilisation of food for growth (§16.4.2.2), and finally, the dependence of the latter on the level of feeding (§16.4.2.3).

16.4.2.1 *Maintenance requirements—determination of ζ and j*

Dawes summarises his findings on the amount of food required to keep plaice of various sizes in a healthy condition but not permitting growth—that is, the daily maintenance ration—in Tables 51 and 52 of his 1930 paper, and Tables 7 and 14 of the 1931 paper. Dawes used fish of both sexes, but they behaved similarly as regards growth and we shall not distinguish between them.

In Table 16.12 are extracted from the above summaries the average weights of the fish (columns A) and their corresponding average daily ration (columns B). We require to fit (9.16) to these data, giving the rate of consumption of maintenance food as a function of body weight, and for this purpose we shall write this equation in the incremental form (cf. (9.16))

$$\frac{\Delta \xi_m}{\Delta t} = \zeta w^j$$

Taking logarithms we have the linear form

$$\log \left(\frac{\Delta \xi_m}{\Delta t}\right) = \log \zeta + j \log w$$

and the data of Table 16.12 have therefore been plotted on logarithmic scales in Fig. 16.14. Fitting by least squares gave the values $\zeta = 20.55$ (in units of a year) and $j = 0.6654$. As mentioned in §9.4.3.1.1, considerable simplification is possible if j can be regarded as having a value which is an exact multiple of one-third. The value of j found above is extremely close to two-thirds and we have adjusted it to

$$j = 0.667$$

the maintenance coefficient becoming

$$\zeta = 20.48$$

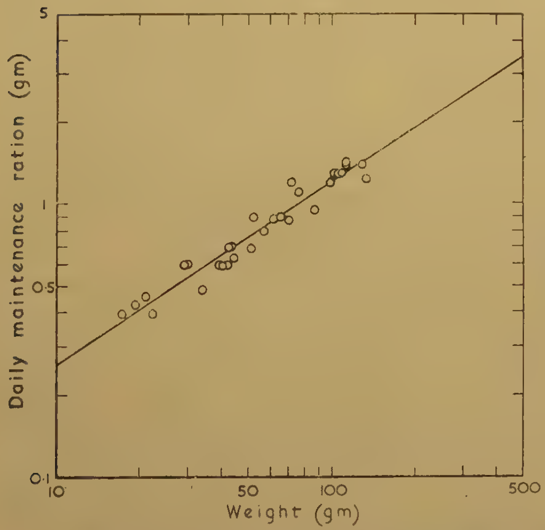

FIG. 16.14 MAINTENANCE REQUIREMENTS OF PLAICE

[Daily maintenance ration plotted against body weight; from Table 16.12. The slope of the line gives the estimate $j = 0.665$, indicating that maintenance requirements are proportional to the two-third power of body weight.]

Although this value of the maintenance coefficient is specific to the type of food used by Dawes (*Mytilus*), it is the one needed to interpret the data presented below on the utilisation of the same food for growth; the value of j however, should be independent of the type of food. On the other hand, it has been pointed out by Allen (1951) that particularly active fish, such as those whose normal habitat is a fast stream, may need somewhat larger maintenance rations in the wild state than would be indicated by feeding experiments in small tanks where movement is much restricted. Plaice can scarcely be regarded as active fish, however, and in Dawes' experiments they were kept in a fairly large container through which water could flow. There is no reason to believe, therefore, that the relative demands of maintenance and growth under any given conditions of feeding were seriously biased in Dawes' experiments.

16.4.2.2 *Utilisation of food for growth—determination of ε*

We shall confine ourselves in this sub-section to an examination of the data referring to three particular fish, which Dawes considered likely to be the most useful for a study of the relationship between growth and growth-food. In Table 16.13, column B, are given the weights of fish D3, B1 and B4 at approximately fortnightly intervals during the experiment. In columns C and D are given the weight increments and the total food eaten during each period, the lengths of the latter in days being given in column E.

Using the values of j and ζ found above, and taking the weight of the fish to be halfway between that at the beginning and at the end of each period, the food utilised for maintenance was calculated (column F) and subtracted from the total food consumed to give the amounts of food used for growth ($\Delta \xi_g$) of column G. Fig. 16.15 shows these values plotted against the corresponding weight increments, Δw, for all these fish. Fitting by the method of least squares the linear regression equation

$$\Delta w = a_0 + a_1 \Delta \xi_g$$

gave $a_0 = +0.54$ and $a_1 = +0.18$. This value of a_1 does not differ significantly from zero, and it is convenient and does not involve significant errors if the adjusted values

$$a_0 = \text{zero}$$

and

$$a_1 = \varepsilon = 0.20$$

are used.

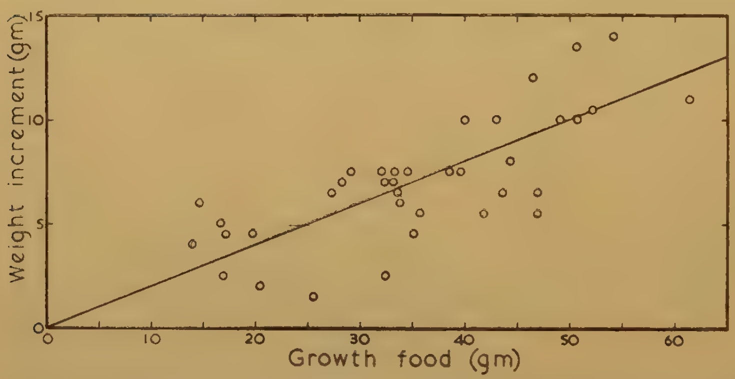

FIG. 16.15
GROWTH AND GROWTH FOOD IN PLAICE

[Growth increment plotted against growth food, i.e. food consumed in excess of maintenance requirements; from Table 16.13, columns C and G. The slope of the line gives the estimate $\varepsilon = 0.2$.]

16.4.2.3 *The relationship between efficiency of food utilisation and level of feeding—determination of ε_0, k, Q, $W_{\infty M}$ and $W_{\infty L}$.*

In §9.4.3.1.2 we discussed the application of Kostitzin's equation relating the net assimilated energy x and the corresponding gross energy intake X, viz.:

$$x = \frac{1}{k} \tanh (k\sigma\xi)$$

and showed that by regarding the net energy x as consisting partly of maintenance energy and partly of energy appearing as growth, we could put

$$x = Q\,\bar{w}^{2/3} + \frac{dw}{dt} = \frac{1}{k} \tanh (k\varepsilon_0 \xi)$$

where Q is the maintenance energy coefficient and ε_0 is the maximum value of ε. For the analysis of data we shall write this equation in the form

$$Q\bar{w}^{2/3} + \frac{\Delta w}{\Delta t} = \frac{1}{k} \tanh \left(k\varepsilon_0 \frac{\Delta \xi}{\Delta t} \right) \quad \ldots \quad \ldots \quad \ldots \quad (16.13)$$

where Δw is a weight increment over a period of time Δt, $\bar{w}$ is the mean weight over that period and $\Delta \xi$ is the corresponding amount of food eaten. As we have shown in §9.4.3.1.3, the maximum possible assimilated energy, $1/k$, itself varies with size of the organism, so that we need to choose Δw and Δt as small as is consistent with the accuracy of the data.

The quantity $Q\bar{w}^{2/3}$ is the rate of utilisation of energy for maintenance, and we have suggested that this does not vary with the level of feeding. If it is measured at the maintenance level of feeding, for example, then we can write

$$Q\bar{w}^{2/3} = \frac{1}{k} \tanh (k\varepsilon_0 \, \zeta \bar{w}^{2/3}) \quad \ldots \quad \ldots \quad \ldots \quad (16.14)$$

Substituting in (16.13) and rearranging gives

$$\frac{\Delta w/\Delta t}{\tanh (k\varepsilon_0 \, \Delta \xi/\Delta t) - \tanh (k\varepsilon_0 \, \zeta \bar{w}^{2/3})} = \frac{1}{k} \quad \ldots \quad \ldots \quad (16.15)$$

If data for food intake and the corresponding weight increments are available, together with a knowledge of the value of the maintenance food coefficient ζ, then (16.15) contains only two unknown quantities, viz.: k and ε_0.

Dawes used seven experimental fish to obtain data of this kind. Three of them, D3, B1 and B4, were supplied with as much food as they would accept. The others—I1, I2, I3 and I4—were fed on restricted rations, which were nevertheless sufficient to allow appreciable growth. We have plotted the weights of each of these seven fish against time in days (measured from the beginning of the experiment) from Dawes' (1931) Tables 67, 68, 69, 34, 35, 36 and 37, and drawn smooth freehand curves through the points. Corresponding curves of the total food eaten by each fish up to various times from the beginning of the experiment were drawn from data given in the same tables. The dates during the experiments when each fish reached weights between 20 and 60 gm. were read off at 5 gm. intervals from the growth curves. The weights at dates 10 days before and 10 days after these mid-dates (i.e. $\Delta t = 0.0548$ years) were then read off, the difference between each pair giving the values of Δw and $\Delta w/\Delta t$ entered in columns C and D respectively of Table 16.14 against the appropriate mid-weight. The amount of food eaten by each fish during these 20 day periods was read off from the corresponding food consumption curves, giving the values of $\Delta \xi$ and $\Delta \xi/\Delta t$ entered in columns E and F respectively. This procedure may be illustrated with reference to the growth and food intake of fish D3, the data relating to which are given in column B and D of Table 16.13 and are shown plotted in the manner described above in Fig. 16.16. For example, this fish reached a weight of 35 gm. on the 52nd day after the beginning of the experiment. Its weight on the 42nd day was 29.0 gm., and on the 62nd, 38.0 gm., giving a value of $\Delta w = 9.0$ gm. entered in column C of Table 16.14 for this fish against the mid-weight of 35 gm. From the food consumption curve we find that it had eaten 81 gm. of food up to and including the 42nd day, and 140 gm. by the 62nd day, giving the value of $\Delta \xi = 59$ gm. entered in the same row of column E.

We must now deal with the problem of fitting (16.15) to the data of Table 16.14 in order to obtain estimates of $1/k$ and ε_0. Values of $\Delta w/\Delta t$ and $\Delta \xi/\Delta t$ referring to fish of any of the weights given in column B, together with the value of $\zeta = 20.48$ found in §16.4.1, can be inserted in (16.15) to calculate the value of $1/k$ for each fish, provided a value of the quantity $k\varepsilon_0$ is also specified. Theoretically there is, for each size of fish, a value of $k\varepsilon_0$ that will give from (16.15) identical values of $1/k$ for each fish of that size, irrespective of its

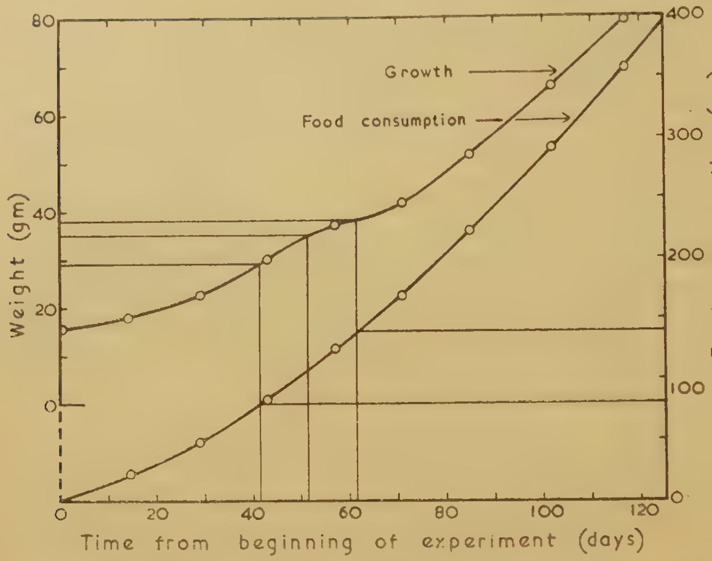

FIG. 16.16
FOOD CONSUMPTION AND GROWTH OF PLAICE D3

[Cumulative food consumption and growth plotted against time from beginning of experiment; from Table 16.13, columns B, D and E. This diagram illustrates the method described in the text of estimating the rate of food consumption of fish as a function of weight (see Table 16.14).]

level of feeding. In practice, bearing in mind the existence of experimental variation, we require the value of $k\varepsilon_0$ that produces, for fish of a given size, values of $1/k$ having the minimum variance. These have been found by trial for each size of fish in column B and are given in column H of Table 16.14. The mean value of $1/k$ for fish of each size is given in column J and the corresponding value of ε_0, obtained by multiplying $k\varepsilon_0$ by $1/k$, is given in column K. It will be remembered that on theoretical grounds we should expect $1/k$ to increase with weight and ε_0 to remain approximately constant, and inspection of columns J and K shows that this is broadly true. A sudden drop in $1/k$ beginning at 40 gm. is noticeable however, and this can be seen to be due largely to the intermediate feeding fish I2 present in the higher weight-groups but absent from the three lowest. In view of such appreciable intrinsic differences in efficiency of utilisation between individual fish we cannot combine estimates of $1/k$ or ε_0 from weight groups comprising different fish without introducing bias.* The procedure we have adopted is therefore to exclude fish I2 altogether, thus leaving weight groups 40, 45, 50 and 55 gm., comprising the same six fish, three of which are maximum feeding fish and three intermediate. The determination of $1/k$ and ε_0 by the same minimum variance method was then repeated for these four weight groups, the resulting values being summarised in columns D and E respectively of Table 16.15.

It is interesting to see whether the resulting change in $1/k$ with weight is of the form we should expect, and to test this we may use the relationship deduced in §9.4.3.1.2, viz.:

$$\frac{1}{k} = Q\bar{w}^{2/3} + 3K\,(\bar{w}^{2/3}\,W_{\infty M}^{1/3} - \bar{w}) \quad .. \quad .. \quad (16.16)$$

Taking the mean value of $W_{\infty M}^{1/3}$ and of Q found below for the four weight groups in question, viz.:

$$Q = 10.05$$

$$W_{\infty M}^{1/3} = 67.6 \text{ gm.}$$

the predicted curve of $1/k$ against $\bar{w}$ shown in Fig. 16.17 was obtained. In this figure the values of $1/k$ from column D of Table 16.15 are shown by circles, the original values for all the weight groups of column J of Table 16.14 being indicated by crosses, although it must be remembered that the line is not fitted to the latter points. It is seen that exclusion of fish 12 has made the data as a whole more homogeneous, and we may conclude that the theoretical curve provides a satisfactory representation of the data.

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*A further—and perhaps more serious—difficulty is that different fish make up the maximum feeding and intermediate feeding groups, but this is a limitation of the experimental design used by Dawes.

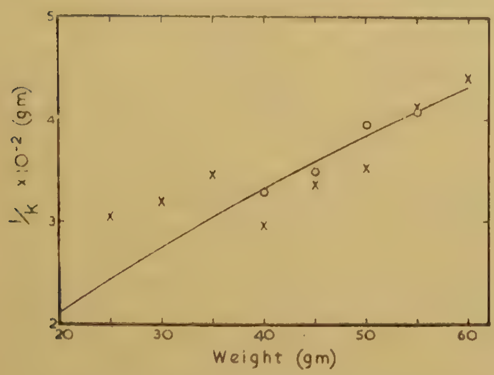

FIG. 16.17 MAXIMUM NET ASSIMILATED ENERGY IN PLAICE

[Maximum net assimilated energy, $1/k$, plotted against body weight, with the curve predicted from Kostitzin's equation. The crosses are from Table 16.14, column J, and refer to all the experimental fish; the circles are from Table 16.15, column D and refer to the same six fish throughout.]

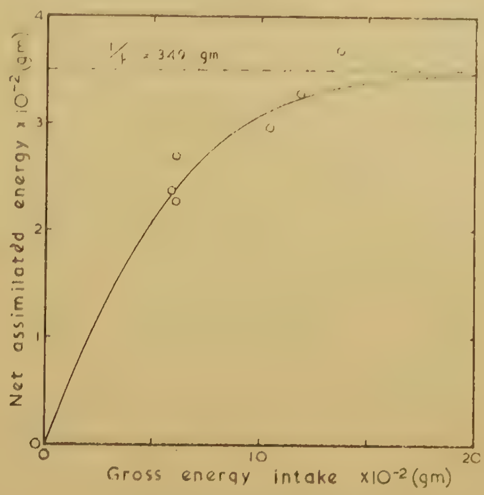

FIG. 16.18 GROSS AND NET ENERGY IN PLAICE

[Net assimilated energy of 45 gm. fish plotted against gross energy intake and the curve predicted from Kostitzin's equation with parameter values $\varepsilon_0 = 0.485$, $1/k = 349$ gm., the latter being the asymptote to which the curve tends.]

It is worthwhile to derive estimates of the net and gross energy intakes for fish of a particular weight and to see how they are fitted by the original form of Kostitzin's equation

$$x = \frac{1}{k}\tanh(k\varepsilon_0\,\xi)$$

Observed values of x are obtained from the expression

$$x = Q\bar{w}^{2/3} + \frac{\Delta w}{\Delta t}$$

where $Q = 10.05$ (see below) and $\Delta w/\Delta t$ has the values of column D of Table 16.14 for 45 gm. fish (i.e. $\bar{w} = 45$ gm.). These values are shown in Fig. 16.18, the line being drawn from Kostitzin's original equation using the values $k\,\varepsilon_0 = 0.00139$ and $1/k = 349$ for 45 gm. fish of Table 16.15. The horizontal broken line is the asymptotic value to which x tends as $X \to \infty$, i.e. $1/k = 349$. Bearing in mind the small number of fish involved the fit is satisfactory.

It will be remembered that the parameter $1/k$ does not appear explicitly in the final equations such as (9.32), but that we require instead to estimate the maintenance energy coefficient Q and the quantity $W_{\infty M}$, the latter being the maximum weight towards which a fish would grow if it could assimilate energy at the maximum possible rate throughout its life.

To estimate Q we use the relationship deduced in §9.4.3.1.2, viz.:

$$Q = \zeta\varepsilon_m$$

where ε_m is the efficiency of utilisation at the maintenance level of feeding and is given by the equation

$$\varepsilon_m = \frac{x_m}{X_m} = \frac{1}{k\xi_m} \tanh (k\varepsilon_0 \, \xi_m) = \frac{1}{k\zeta\bar{w}^{2/3}} \tanh (k\varepsilon_0 \, \zeta\bar{w}^{2/3})$$

Using the same values of ζ, ε_0 and $1/k$ as before—the last two being from Table 16.15—this expression gives the values of ε_m entered in column F of the same table, which it will be seen are consistently lower than those of ε_0 in column E, as would be expected. The mean value of ε_m is 0.49, from which we calculate a value of

$$Q = 20.48 \times 0.49 = 10.05$$

To estimate $W_{\infty M}$ we use (16.16) and substitute for $Q\bar{w}^{2/3}$ from (16.14), thus obtaining

$$\frac{1}{k} = 3K\bar{w}^{2/3} \, W_{\infty M}^{1/3} + \frac{1}{k} \tanh (k\varepsilon_0 \, \zeta\bar{w}^{2/3}) - 3K\bar{w}$$

so that we have

$$W_{\infty M}^{1/3} = \frac{1 - \tanh (k\varepsilon_0 \, \zeta\bar{w}^{2/3}}{3kK\bar{w}^{2/3}} + \bar{w}^{1/3} \quad .. \quad .. \quad (16.17)$$

Using the values of $1/k$ in column D of Table 16.15, the mean of the estimates of ε_0 (0.51) and with the same value of ζ as before, (16.17) gives the values of $W_{\infty M}^{1/3}$ in column G of the same table. The average of these is 67.6 gm., corresponding to a value of

$$W_{\infty M} = 309{,}000 \text{ gm.}$$

which we use in subsequent calculations.

It will be appreciated that the parameter $W_{\infty M}$ is essentially of theoretical significance only, in that a fish could never grow so fast that its growth could be described by this value of W_∞ ; in other words, a fish cannot actually assimilate energy at the maximum possible rate $1/k$, since to do so it would have to consume food infinitely fast. When dealing with the problem of feeding intensity in §9.4.3.2.2, we found it necessary to specify a parameter $W_{\infty L}$ to define the maximum growth rate that a fish could attain in practice if presented with an unlimited supply of food. An approximate estimate of it can be obtained from the data in Table 16.13 referring to the growth of the maximum feeding fish D3, B1 and B4.

Denoting by w_1 and w_2 the weights of a maximum feeding fish at the beginning and end respectively of the experiment of duration t_{12}, we have from the von Bertalanffy equation

$$W_{\infty L}^{1/3} = \frac{w_2^{1/3} - w_1^{1/3} \, e^{-Kt_{12}}}{1 - e^{-Kt_{12}}} \quad .. \quad .. \quad .. \quad .. \quad (16.18)$$

Table 16.16 (columns B, C and D) gives the values of w_1, w_2 and t_{12} for each of the above fish, and these substituted in the above equation give the estimates of $W_{\infty L}^{1/3}$ entered in column E, having a mean of 48 gm., so that $W_{\infty L}$ is about 110,000 gm. Now in many fish, including plaice, growth slows down or even ceases during the winter months, and it will be seen from column C of Table 16.13 that this is so even under experimental conditions of abundant food supply. It is probable, therefore, that the growth over the experimental period of Table 16.13 is very nearly equal to the total growth attainable over the period of a full year at the maximum feeding level. A more appropriate value of $W_{\infty L}$ may consequently be obtained by putting $t = 1$ in (16.18), giving the estimates of column F. These have a mean of $W_{\infty L}^{1/3} = 25$ gm., corresponding to a value of $W_{\infty L} = 16{,}000$ gm. which we shall use in subsequent calculations.

It will be noted that the whole of the above analysis of maintenance and growth requirements deals essentially with net energy assimilation, and the particular food used is largely irrelevant to it. The one exception concerns the limiting growth parameter $W_{\infty L}$, since in order to use the above estimate in theoretical population models it is necessary to assume that the limiting consumption of gross energy is independent of the type of food (see §9.4.3.2.4). Since Dawes used *Mytilus* flesh throughout his experiments it is not possible to test this assumption from his data, but it is probable that this food has a higher nutritional value than the mixture of foods typically found in plaice stomachs. Thus Rinke's (1937) data give the ratio of dry organic weight to total weight for *Mytilus* flesh as about 0.2, whereas Petersen (1918) gives a value of about 0.1 for a typical mixture of natural foods. Taking this ratio as a rough index of nutritional value (in the absence of direct growth comparisons), and with *Mytilus* flesh as reference, the value of the nutritional factor ν for the natural food mixture can be taken as about 0.5. Thus with the opposite extreme hypothesis that consumption is limited purely by bulk, the value of $W_{\infty L}$ under natural conditions would be of the order of half the above value, i.e. 8000 gm.

Now, reasons were put forward in §9.4.3.2.4 for believing that in practice both bulk and gross energy contribute to limiting the consumption of a given food, so that the true value of $W_{\infty L}$ probably lies between these extremes. Thus it is, in any case, very much larger than the W_∞ observed during the pre-war state (2867 gm.), a value which is itself at the upper end of the important range of W_∞ since we shall be concerned primarily with higher densities than those found before the war. The exact value of $W_{\infty L}$ is therefore not critical (that of $W_{\infty M}$ being even less so); for the present it is best to take the higher value of $W_{\infty L} = 16000$ gm., since if any small bias is thereby involved it will tend to exaggerate the effect of density on growth, and thus ensure that the regulative value of reducing fishing intensity or increasing mesh size is not over-emphasized (cf. the problem of estimating the natural mortality coefficient for haddock in §14.3.2.4).

PART IV

The use of Theoretical Models in a study of the Dynamics and Reaction to Exploitation of Fish Populations

In the last part of this paper we shall be investigating the properties of population models developed in Parts I and II, and applying our findings to problems of fishery regulation. The characteristics of a fish population which are relevant to a study of its reaction to exploitation have been discussed in §5, where it was shown that they could be described by equations which follow as direct extensions of the methods used to derive the basic equation for yield (4.4). It may be helpful to review briefly these characteristics before proceeding.

That which is undoubtedly of the greatest general importance is the *annual yield in weight* (Y_W) under equilibrium conditions. Also important, economically, is the *annual mean biomass of the exploited phase of the population* ($\bar{P}'_W$), because of its direct relation with the catch per unit effort. The *mean weight of fish in the catch* ($\bar{W}_Y$) will be of commercial interest in many cases. The remaining population characteristics requiring consideration are primarily of biological interest. They include the *annual mean biomass* ($\bar{P}_W$), and the *annual mean number* ($\bar{P}_N$), of the whole post-recruit phase of the population. These, as we have seen in Part III, need to be evaluated in connection with the relation between population parameters such as growth, natural mortality and recruitment, and population density. There are, finally, the *mean length* ($\bar{L}_Y$) and the *mean age* ($\bar{T}_Y$) of fish in the catch, which may in some cases be valuable as ready indices of the state of the population.

The characteristics of fishing activity, on the other hand, are described by a knowledge of the *fishing mortality* (F) and *age at entry to the exploited phase* ($t_{\rho'}$), which are related to fishing intensity and mesh size, respectively, in the ways already discussed. It is argued in §19.1.1 that all methods of fishery regulation that have been put forward reduce, in effect, to variation of one or other of these quantities; consequently we are interested, for the most part, in observing the behaviour of the population characteristics defined above as the magnitude of one or both of them is varied.

To interpret the properties of population models in this way it is necessary in the first instance to insert, for the relevant parameters, values which refer to some real population. As mentioned in the introduction to Part III, the stock with which we are primarily concerned here is the North Sea plaice, though we have made some use of information relating to the North Sea haddock (§§17.7, 18.3.2, 18.4.1, 18.5.2 and 18.6). In each case the parameter values used are those that have been determined in Part III. Some reiteration of the principles of the theoretical methods developed in Parts I and II will be found here—especially in §18—thus avoiding much reference back.

The behaviour of the simple population models of Part I is investigated in §17. In these, the population parameters are assumed to be constant, and we see how far it is possible to state general properties of the curves describing the population characteristics as functions of fishing mortality and age at entry to the exploited phase. An important aspect of this problem is the analysis of the effect on the shape of such curves of different values of particular population parameters. Such an analysis, as well as contributing to the understanding of the behaviour of the models, allows some appreciation to be made of the significance of possible errors in the values of certain parameters. The section is concluded by a review of the theoretical models developed by previous authors.

In §18 we investigate the extent to which the provisional conclusions of §17 need modifying when the more comprehensive models of Part II are considered. Thus we need to know the result of more precise treatments of situations to which a simple approximation had previously been made. Examples include the effects of the detailed representation of a mesh selection ogive, and of the recruitment pattern in the plaice arising through differences in weight of fish at the same age. The rest of §18 concerns the interdependence of population parameters, as opposed to the simple independent treatment which is adopted in §17. Of particular interest here is the dependence of growth, natural mortality, and recruitment, on population density.

In §19 the conclusions of §§17 and 18 are generalised, and then applied to problems of fishery regulation. Although the problems discussed here are largely practical ones, it has been found that certain additional concepts and methods of analysis are required; the aims of §19 are therefore to establish the general principles on which regulation should be based, and to offer technical comment on the various methods that have been suggested.

In §§17 and 18, where the plaice and haddock fisheries are considered individually, it is necessary to refer on a number of occasions to the kind of changes in fishing activity which would apparently have given better results from these fisheries than were obtained during the pre-war years. It must be stressed that mention of such changes in this context is in no sense to be taken as advice on regulatory procedure; apart from being premature in view of the fact that the principles of fishery regulation are not discussed until §19, regulation of the North Sea demersal fisheries must be conceived as a whole and not determined by what is best for two of the many species involved, even though they are two of the most important. In the last section of this paper (§20), provisional assessments for the cod and sole are therefore introduced, and an attempt is then made to establish the requirements for regulation of the North Sea demersal fisheries as they appear in the light of present knowledge.

SECTION 17:
APPLICATION OF POPULATION MODELS OF PART I

17.1 Methods of Calculation

To those who are not familiar with the technique, the calculation of population characteristics from equations such as those derived in §§4 and 5 may present certain difficulties, and the following comments may be helpful. The first need, from the point of view of both speed and accuracy, is for an efficient work-sheet. For example, the summation term from $n = 0$ to 3 which appears in all equations involving the weight of fish, is almost certain to lead to computational errors and much loss of time if some orderly procedure is not adopted.

In Fig. 17.1 is shown an example of the work-sheet, based on the plaice, which the authors have found by experience to be satisfactory for the computation of most of these equations as functions of F, and which can also serve as a basis for the more elaborate calculations referred to in §§18 and 19. It has been found that an experienced computer using a hand calculating machine can complete the calculation shown in Fig. 17.1 in about three hours. It will be seen that this work-sheet contains a number of values of F, but only one of $t_{\rho'}$. If the calculation is repeated for each of a series of values of $t_{\rho'}$ then the results will show the variation of the population characteristics in question as functions of either F or $t_{\rho'}$ or both. A series of work-sheets of this kind was used to prepare the isopleth diagrams of Figs. 17.14—17.17 in which both F and $t_{\rho'}$ are treated as variables. The work-sheet itself is self-explanatory; it will be noticed that the four summation terms, two of which are negative and two positive, are arranged so as to facilitate the processes of addition and subtraction that are required near the end of the calculation. The only calculations in the equations of §§4 and 5 which this work-sheet does not cover are those concerned with the first terms of the equations for annual mean biomass ($\bar{P}_W$) and mean number in

FIG 17.1

SPECIES: PLAICE

EQUATIONS

$$\frac{\bar{P}'_N}{R} = \frac{e^{-M\rho}}{F+M}\left(1 - e^{-(F+M)\lambda}\right) \; ; \quad \frac{Y_N}{R} = F\frac{\bar{P}'_N}{R} \; ; \quad \frac{\bar{P}'_W}{R} = e^{-M\rho} W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\left(1 - e^{-(F+M+nK)\lambda}\right) \; ; \quad \frac{Y_W}{R} = F\frac{\bar{P}'_W}{R}$$

PARAMETERS

$M = 0.10$
$t_\rho = 3.72$ (yrs.)
$t_{\rho'} = 3.72$ (yrs.)
$\lambda = 15$ (yrs.)
$t_0 = -0.815$ (yrs.)
$W_\infty = 2867$ (gm.)
$K = 0.095$
$q = 0.00892.$

$t_{\rho'} - t_0 = 4.535$ (yrs.)

$t_{\rho'} - t_\rho = \rho = 0.$

$t_\lambda - t_{\rho'} = \lambda = 11.28$ (yrs.)

$e^{-M\rho} \times W_\infty = 2867$ (gm.) = (S).

n	$M + nK$	Ω_n	$\Omega_n e^{-nK(t_{\rho'}-t_0)}$
0	0·100	+ 1	+ 1·0000 = (T_0)
1	0·195	− 3	− 1·9500 = (T_1)
2	0·290	+ 3	+ 1·2675 = (T_2)
3	0·385	− 1	− 0·2746 = (T_3)

	(A)	(B_0)	(C_0)	(D_0)	(E_0)	(F_0)
$n=0$	F	$(A)+M+nK$	$(B_0) \times \lambda$	$1 - e^{-(C_0)}$	$\frac{(T_0) \times (D_0)}{(B_0)} = \frac{\bar{P}'_N}{R}$	$(E_0) \times (A) = \frac{Y_N}{R}$
	0·00	0·10	1·1280	0·6762	6·7620	0·0000
	0·01	0·11	1·2408	0·7108	6·4618	0·0646
	0·05	0·15	1·6920	0·8159	5·4393	0·2720
	0·10	0·20	2·2560	0·8952	4·4760	0·4476
	0·20	0·30	3·3840	0·9661	3·2203	0·6441
	0·30	0·40	4·5120	0·9890	2·4725	0·7418
	0·40	0·50	5·6400	0·9965	1·9930	0·7972
	0·50	0·60	6·7680	0·9989	1·6648	0·8324
	0·73	0·83	9·3624	0·9999	1·2047	0·8794
	0·75	0·85	9·5880	0·9999	1·1764	0·8823
	1·00	1·10	> 10	1·0000	0·9091	0·9091
	1·50	1·60	> 10	1·0000	0·6250	0·9375

	(A)	(B_2)	(C_2)	(D_2)	(E_2)
$n=2$	F	$(A)+M+nK$	$(B_2) \times \lambda$	$1 - e^{-(C_2)}$	$\frac{(T_2) \times (D_2)}{(B_2)}$
	0·00	0·290	3·2712	0·9620	4·2046
	0·01	0·300	3·3840	0·9661	4·0818
	0·05	0·340	3·8352	0·9784	3·6474
	0·10	0·390	4·3992	0·9877	3·2100
	0·20	0·490	5·5272	0·9960	2·5764
	0·30	0·590	6·6552	0·9987	2·1455
	0·40	0·690	7·7832	0·9996	1·8362
	0·50	0·790	8·9112	0·9999	1·6043
	0·73	1·020	> 10	1·0000	1·2426
	0·75	1·040	> 10	1·0000	1·2188
	1·00	1·290	> 10	1·0000	0·9826
	1·50	1·790	> 10	1·0000	0·7081

	(A)	(B₁)	(C₁)	(D₁)	(E₁)
$n=1$	F	$(A)+M+nK$	$(B_1)\times\lambda$	$1-e^{-(C_1)}$	$\frac{(T_1)\times(D_1)}{(B_1)}$
	0·00	0·195	2·1996	0·8893	— 8·8930
	0·01	0·205	2·3124	0·9009	— 8·5695
	0·05	0·245	2·7636	0·9369	— 7·4570
	0·10	0·295	3·3276	0·9641	— 6·3729
	0·20	0·395	4·4556	0·9884	— 4·8794
	0·30	0·495	5·5836	0·9962	— 3·9244
	0·40	0·595	6·7116	0·9988	— 3·2734
	0·50	0·695	7·8396	0·9996	— 2·8046
	0·73	0·925	> 10	1·0000	— 2·1081
	0·75	0·945	> 10	1·0000	— 2·0635
	1·00	1·195	> 10	1·0000	— 1·6318
	1·50	1·695	> 10	1·0000	— 1·1504

	(A)	(B₃)	(C₃)	(D₃)	(E₃)
$n=3$	F	$(A)+M+nK$	$(B_3)+\lambda$	$1-e^{-(C_3)}$	$\frac{(T_3)\times(D_3)}{(B_3)}$
	0·00	0·385	4·3428	0·9870	— 0·7040
	0·01	0·395	4·4556	0·9884	— 0·6871
	0·05	0·435	4·9068	0·9926	— 0·6266
	0·10	0·485	5·4708	0·9958	— 0·5638
	0·20	0·585	6·5988	0·9986	— 0·4687
	0·30	0·685	7·7268	0·9995	— 0·4007
	0·40	0·785	8·8548	0·9999	— 0·3498
	0·50	0·885	9·9828	0·9999	— 0·3103
	0·73	1·115	> 10	1·0000	— 0·2463
	0·75	1·135	> 10	1·0000	— 0·2419
	1·00	1·385	> 10	1·0000	— 0·1983
	1·50	1·885	> 10	1·0000	— 0·1457

(A)	(P)	(Q)	(R)	(U)	(V)	(W)
F	$(E_0)+(E_1)+(E_2)+(E_3)$	$(P)\times(S)=\frac{\bar{P}'_W}{R}$(gm.)	$(A)\times(Q)=\frac{Y_W}{R}$(gm.)	$\frac{(R)}{194\cdot43}$	$\frac{(Q)}{(E_0)}=\bar{W}_Y$(gm.)	$\frac{68\cdot5}{(E_0)}\{(E_0)+\frac{1}{3}(E_1)\}-\bar{L}_Y$(cm.)
0·00	1·3696	3926·64	0·00	0	580·7	38·47
0·01	1·2870	3689·83	36·90	0·1898	571·0	38·22
0·05	1·0031	2875·89	143·79	0·7395	528·7	37·20
0·10	0·7493	2148·24	214·82	1·1049	479·9	35·99
0·20	0·4486	1286·14	257·23	1·3230	399·4	33·90
0·30	0·2929	839·74	251·92	1·2957	339·6	32·26
0·40	0·2060	590·60	236·24	1·2150	296·3	31·00
0·50	0·1542	442·09	221·05	1·1369	265·6	30·03
0·73	0·0929	266·34	194·43	1·0000	221·1	28·56
0·75	0·0898	257·46	193·10	0·9932	218·9	28·45
1·00	0·0616	176·61	176·61	0·9083	194·3	27·52
1·50	0·0370	106·08	159·12	0·8184	169·7	26·47

FIG 17.1 METHOD OF COMPUTING YIELD EQUATIONS

[Example of work-sheet used in computing characteristics of the exploited phase for various values of F in the steady state from the simple models of Part I. This work-sheet refers to plaice, for a 70 mm. mesh ($t_{\rho'} = 3.72$ yrs.), with parameter values listed at the top. The figures of yield per recruit, Y_W/R, of column (R) are plotted in Fig. 17.2 giving a yield—intensity curve that is referred to in later parts of §§17 and 18 as curve (a). Note that in cases where $t_{\rho'} > t_\rho$, column (E_0) has to be multiplied by $e^{-M\rho}$ to give $\bar{P}'_N/R$].

the population ($\bar{P}_N$), viz.:

$$RW_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_\rho - t_0)}}{M + nK} \left(1 - e^{-(M + nK)\rho}\right)$$

and

$$\frac{R}{M}\left(1 - e^{-M\rho}\right)$$

respectively. These refer to the pre-exploited phase of the population, and consequently do not contain *F*. They may be calculated by methods similar to those set out in the work-sheet and, for each value of $t_{\rho'}$, provide constant quantities to be added to those of $\bar{P}'_W$ and $\bar{P}'_N$ for each value of *F*.

A word may be said here on the standard of precision at which we have aimed in the calculations undertaken for this paper. For the most part we have used four-figure tables of exponential functions, supplementing them occasionally by six-figure tables. This gives results that are, in general, correct to four significant figures. We do not suggest for a moment that this degree of precision corresponds to the accuracy of the parameter estimates on which the calculations are based, but we have found that certain operations—more particularly some of those encountered in §18—can lead to serious inconsistencies if anything less than a four-figure standard of precision in computation is adopted.

The question of checking also raises some difficulties when a very large number of calculations is attempted. A systematic double calculation is not entirely satisfactory, and in the present investigation the labour involved would have been altogether excessive. We have therefore relied mainly on graphical methods of checking, since nearly all the expressions developed in this paper give smooth curves when plotted against *F* or $t_{\rho'}$, as the case may be. This does not, however, cover the possibility of errors arising in the preliminary calculations shown at the top of the work-sheet of Fig. 17.1, since these do not involve *F*, and it has been found best to check these directly.

17.2 VARIATION OF POPULATION AND CATCH CHARACTERISTICS WITH *F*

Fig. 17.2 shows the variation of annual yield in weight per recruit of plaice with fishing mortality under equilibrium conditions computed from (4.4). The values from which it is drawn are those of column (R), Fig. 17.1, and the values of the parameters are listed in the legend; the latter are used for all subsequent calculations unless otherwise stated. It will be remembered that they have been determined from data referring to the pre-war years during which the plaice population was effectively in a steady state; in particular, taking $t_{\rho'}$ as constant at 3.72 years implies the use of a 70 mm. cod-end mesh throughout. The mean pre-war value of the fishing mortality is shown by a broken line. The fact that the values

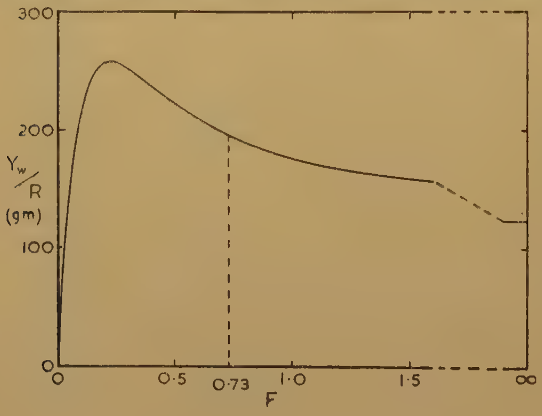

FIG. 17.2 PLAICE: YIELD AGAINST FISHING MORTALITY, 70 MM. MESH

[Steady yield per recruit, Y_W/R, as a function of fishing mortality coefficient *F*, with $t_{\rho'} = 3.72$ yrs.; from Fig. 17.1, column (R). Parameter values used to construct this curve are given at the top of Fig. 17.1. The vertical broken line at $F = 0.73$ indicates the point on the curve corresponding to the pre-war fishing intensity, a procedure that is followed in subsequent diagrams where relevant. An important feature of this curve is that it has a maximum at a value of *F* considerably less than the pre-war value.]

of parameters (other than F) in the equation from which this curve has been calculated have been taken as constant means that these values are assumed to be unaffected by any change in fishing mortality, and hence in density of the population. The yield for any value of F can reasonably be regarded as a mean annual yield over a period of years during which the magnitudes of the parameters have been fluctuating about mean values equal to those used in the calculation. This proposition was shown in §6.2 to be exactly true for recruitment, and is an adequate approximation for the remaining factors provided variations in them are not too great.

A point of great importance concerns the units in which the annual yield is expressed. All the equations of Parts I and II in which the annual number of recruits R appears, with the exception of those of §6.1.3 defining self-regenerating population models, may be very simply transformed to give, instead of the absolute value of the population characteristic in question (whether it be yield, biomass, etc.) the value *per recruit* Y_W/R, $\bar{P}_W/R$, etc. There are two reasons why such a transformation is desirable at this stage. Firstly, the annual number of recruits is a quantity seldom, if ever, open to direct observation; thus the estimates of R given in §15.2.1 have, in fact, been obtained by dividing the actual annual yield by the appropriate value of the yield per recruit. More important, however, is that the particular value of R has no effect whatever on the *shape* of any of the curves of the population characteristics with which we are concerned in this section, but only on their absolute levels. This can be seen at once from (4.4) by the fact that the differential $\partial Y_W/\partial R$ is independent of R (so long as R is regarded as constant or, at least, independent of the other parameters). Although many conclusions concerning the exploitation of fish populations can be reached by reference to the behaviour of the yield per recruit, there are two important aspects of the problem for which absolute units of yield are essential. One of these concerns the dependence of number of recruits on population density, when R is, specifically, no longer a constant. The other arises when dealing with the economic aspects of a commercial fishery, for which it is necessary to know the absolute yield even though R may be a constant. In this latter case it is also necessary, at some stage, to transform the fishing mortality coefficient into fishing intensity. These points are discussed in §§17.6 and 19.1.

We may now examine the shape of the yield curve of Fig. 17.2 in more detail, since, despite the simplicity of the assumptions on which it is based, it serves to illustrate important features of the behaviour of exploited fish populations.

(a) The curve starts at the origin; that is, the yield is zero when the fishing mortality is zero, as is required.

(b) As F increases from zero so does Y_W/R, very rapidly at first, though at a continually decreasing rate.

(c) A maximum value of the yield, $(Y_W/R)_{\max}$, is reached at a certain value of fishing mortality, $(F)_{\max}$.

(d) Thereafter the curve descends comparatively slowly, with the slope decreasing towards an asymptotic yield as $F \to \infty$. It will be noted that this limiting yield per recruit is in fact the weight of a fish when it enters the exploited phase, since with an infinitely high fishing intensity all fish are caught immediately they reach this age.

In describing changes in yield with F it must be borne in mind that this curve relates to equilibrium yields, and gives no information on the actual changes in yield *in time*, following an actual change in fishing intensity. Such matters are dealt with in §19.2.2 where transitional phases are discussed.

Further information can be gained by considering the behaviour of the catch per unit fishing intensity, which is proportional to the yield per recruit per unit fishing mortality, Y_W/FR, which in turn is equal to the annual mean biomass per recruit of the exploited phase of the population, $\bar{P}'_W/R$. In Fig. 17.3 is shown the curve of $\bar{P}'_W/R$ as a function of F given by (5.6). It decreases continuously from a finite value at $F = 0$, rapidly at first and then flattening to an asymptote at zero as $F \to \infty$. Since, in plaice, $t_p = t_{p'}$ (see §15.1.4) this curve is the same as that of the annual mean biomass of the whole post-recruit phase, $\bar{P}_{W'}/R$, as a function of F; the difference in the behaviour of these two characteristics is therefore shown for haddock in §17.7, since in this species t_ρ is not equal to $t_{\rho'}$. Again the broken line shows the pre-war fishing mortality of 0.73. It seems then from Figs. 17.2 and 17.3 that with a rather lower fishing intensity than this a rather greater yield could have been obtained, and the catch per unit effort increased considerably.

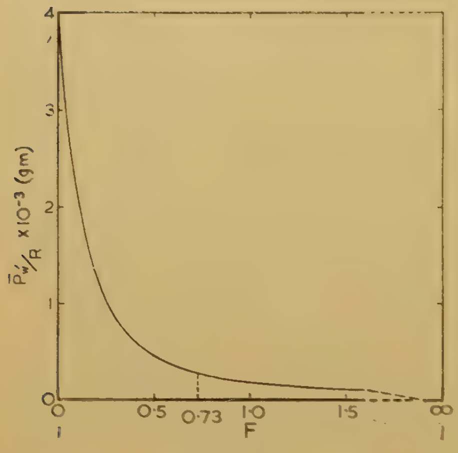

FIG. 17.3 PLAICE:
BIOMASS AGAINST FISHING MORTALITY, 70 MM. MESH

[Biomass per recruit of the exploited phase, $\bar{P}'_{W'}/R$ (proportional to catch per unit effort) as a function of fishing mortality coefficient F with $t_{\rho'} = 3.72$ yrs.; from Fig. 17.1, column (Q). With a 70 mm. mesh this is also the curve of biomass of the whole post-recruit phase, since in these circumstances $t_{\rho'} = t_\rho$.]

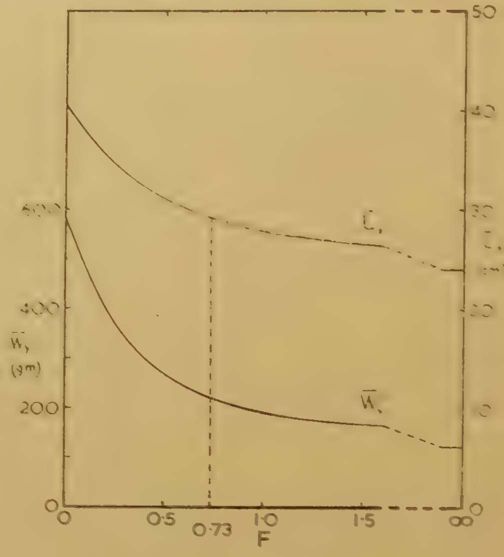

FIG. 17.4 PLAICE:
MEAN WEIGHT AND LENGTH AGAINST FISHING MORTALITY, 70 MM. MESH

[Mean weight, $\bar{W}_Y$, and length, $\bar{L}_Y$, of fish in the catch as functions of F with $t_{\rho'} = 3.72$ yrs.; from Fig. 17.1, columns (V) and (W).]

Turning now to the average weight of fish in the catch, $\bar{W}_Y$ [Fig. 17.4, from (5.12)], which it will be remembered is the same as that in the exploited phase of the population, we see that this also decreases continuously from a finite value at $F = 0$ to an asymptote as $F \to \infty$. This asymptote is the mean weight of fish at age $t_{\rho'}$, i.e. it is the same as Y_W/R at $F = \infty$. The mean length of fish in the catch, $\bar{L}_Y$, computed from (5.10), varies in a similar way.

The remaining characteristics need less comment. They are the annual mean numbers of the exploited phase of the population, $\bar{P}'_N/R$, [Fig. 17.5, from (5.3)]; the mean annual catch in number per recruit, Y_N/R, [Fig. 17.6, from (5.9)], and the mean age of fish in the catch, $\bar{T}_Y$, [Fig. 17.7, from (5.14)]. The curve of $\bar{P}'_N/R$ is similar in shape to that of $\bar{P}'_{W'}/R$; that of Y_N/R, however, differs from the corresponding curve of yield in weight in that it tends to an upper asymptote and has no peak. This important difference should be noted in view of the fact that the curves have been calculated from equations which are identical except that (5.9) contains no reference to growth.

17.3 Variation of Population and Catch Characteristics with $t_{\rho'}$

In the previous section we were concerned with changes in population characteristics corresponding to different values of fishing mortality, with the value of $t_{\rho'}$ held constant throughout and corresponding to a 70 mm. cod-end mesh. We now perform the converse operation, that is to hold the fishing mortality constant at $F = 0.73$ and vary the value of $t_{\rho'}$, the values of the other population parameters remaining unchanged.

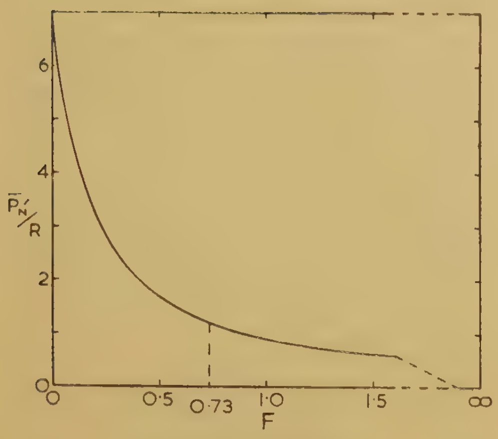

FIG. 17.5 PLAICE: POPULATION SIZE AGAINST FISHING MORTALITY, 70 MM. MESH

[Population number per recruit of the exploited phase $\bar{P}'_N/R$, as a function of F with $t_{\rho'} = 3.72$ yrs.; from Fig. 17.1, column (E_0).]

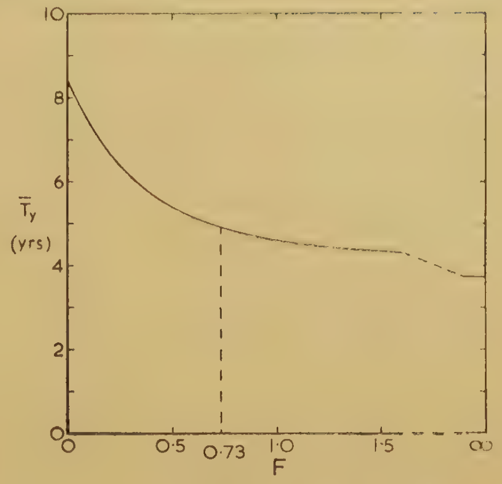

FIG. 17.7 PLAICE: MEAN AGE OF FISH AGAINST FISHING MORTALITY, 70 MM. MESH

[Mean age of fish in the catch and exploited phase, $\bar{T}_Y$, as a function of F with $t_{\rho'} = 3.72$ yrs.]

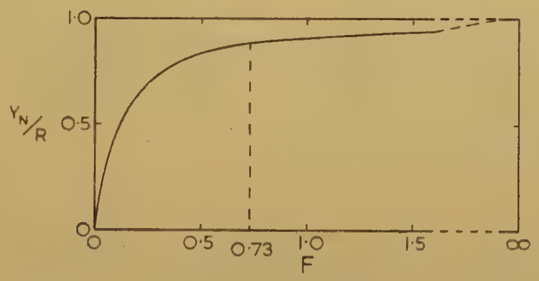

FIG. 17.6 PLAICE: YIELD IN NUMBER AGAINST FISHING MORTALITY, 70 MM. MESH

[Yield in number per recruit, Y_N/R, as a function of F with $t_{\rho'} = 3.72$ yrs.; from Fig. 17.1, column (F_0). Unlike the curve of yield in weight (Fig. 17.2), the yield in number curve does not have a mode].

Fig. 17.8 shows the variation in mean annual yield in weight per recruit, Y_W/R, with $t_{\rho'}$. The most noticeable feature of this curve is the existence of a maximum value of Y_W/R more pronounced than in the corresponding curve of Y_W/R as a function of F (Fig. 17.2). The curve begins at age t_ρ at which fish enter the exploited area and since, in plaice, the pre-war mesh was such that fish were then liable to capture, the point at which it starts on the left hand boundary is also the value of Y_W/R corresponding to the pre-war mesh. The curve reaches zero at a value of $t_{\rho'} = t_\lambda$, implying that a mesh of a size corresponding to this or a higher value of $t_{\rho'}$ would be so large that no fish would be retained by it during their life-span. We may note at this point that the right-hand side of curves describing the behaviour of population characteristics as functions of $t_{\rho'}$ are likely to depend somewhat critically on the particular value of t_λ that has been taken, but we shall look into this point in more detail in §17.5.2.

The behaviour of $\bar{P}'_W/R$ and $\bar{P}_W/R$ with respect to changes in $t_{\rho'}$ (Fig. 17.9) is very different from that with respect to changes in F. Thus $\bar{P}'_W/R = \bar{P}_W/R$ when $t_{\rho'} = t_\rho$, but with increasing values of $t_{\rho'}$, $\bar{P}_W/R$ rises to a maximum and then falls to zero as $t_{\rho'}$ approaches t_λ. This is because $\bar{P}'_W/R$ is the annual mean biomass of the exploited phase,

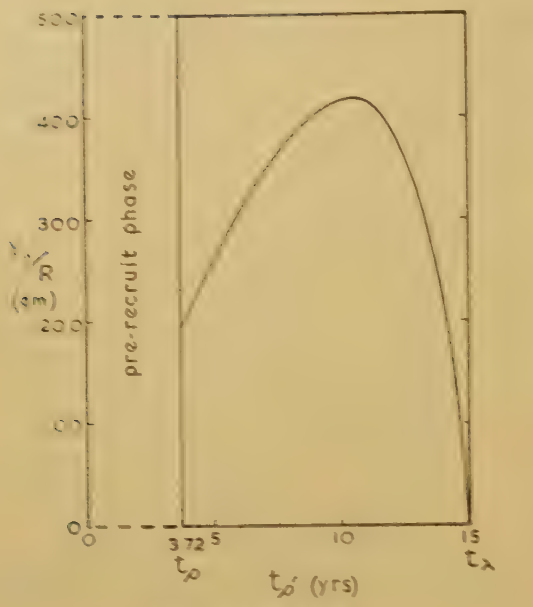

FIG. 17.8 PLAICE:
YIELD AGAINST MESH, PRE-WAR
FISHING INTENSITY

[Yield per recruit, Y_W/R, as a function of mean selection age, $t_{\rho'}$, with $F = 0.73$. The corresponding scale of mesh size, if growth is assumed to be density independent, can be constructed from Fig. 15.13 and is shown here below the $t_{\rho'}$ scale (see, however, Fig. 18.11 for effect of density dependent growth). The maximum of the curve occurs at a value of $t_{\rho'}$ considerably above that for a 70 mm. mesh (3.72 yrs.).]

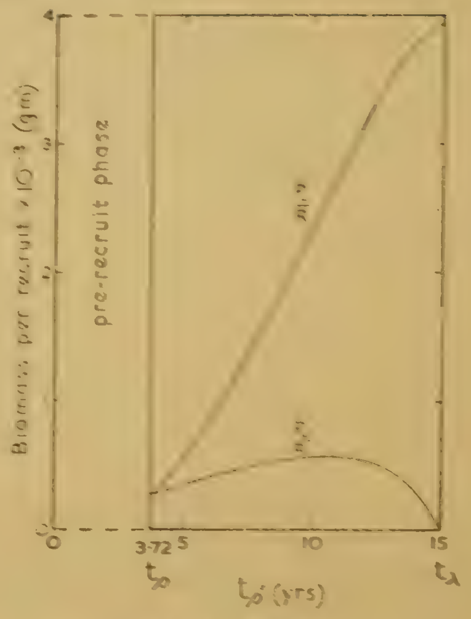

FIG. 17.9 PLAICE:
BIOMASS AGAINST MESH, PRE-WAR
FISHING INTENSITY

[Biomass per recruit of the exploited phase, P'_W/R, and total biomass per recruit, $\bar{P}_W/R$, as functions of $t_{\rho'}$ with $F = 0.73$.]

and with $t_{\rho'}$ very nearly equal to t_λ, the exploited phase is only a very small fraction of the total population. $\bar{P}_W/R$, on the other hand, increases continuously to a finite value—the biomass of the unexploited population—at $t_{\rho'} = t_\lambda$, and is there the same as the value of $\bar{P}_W/R$ for $F =$ zero in Fig. 17.3.

Fig. 17.10 shows that the mean weight $\bar{W}_Y$, and length $\bar{L}_Y$, of fish in the catch increase continuously with $t_{\rho'}$. The picture is completed by the curves of $\bar{P}_N/R$, $\bar{P}_N'/R$, Y_N/R, and $\bar{T}_Y$ as functions of $t_{\rho'}$, which are shown in Figs. 17.11, 17.12 and 17.13.

17.4 SIMULTANEOUS VARIATION OF F AND $t_{\rho'}$; THE YIELD ISOPLETH DIAGRAM

In the preceding two sections we have investigated the variation of population characteristics in particular circumstances; firstly with respect to F for a certain value of $t_{\rho'}$, and secondly with respect to $t_{\rho'}$ for a certain value of F. We must now see to what extent the resulting behaviour was dependent on the particular values of $t_{\rho'}$ or F that were selected to remain constant. This leads to more general conclusions concerning the behaviour of the plaice population under conditions in which both F and $t_{\rho'}$ are changed simultaneously.

Since there are now three variables to represent, we shall do this by plotting F and $t_{\rho'}$ on the X and Y axes respectively, and draw lines through numerically equal values of the population characteristics in question generated by pairs of values of F and $t_{\rho'}$. In this way we obtain a form of contour map, which will be referred to as an *isopleth diagram**. (Beverton, 1953).

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*The term 'isopleth' has been used by D'Arcy Thompson (1948), is regularly used by hydrographers, and seems preferable to 'contour' as it has a more general meaning. Yield isopleths have also been computed for the Georges Bank haddock (see H. W. Graham, 1953), and for the winter flounder (*Pseudopleuronectes americanus* Walbaum) of Nova Scotia by Dickie and McCracken (1955).

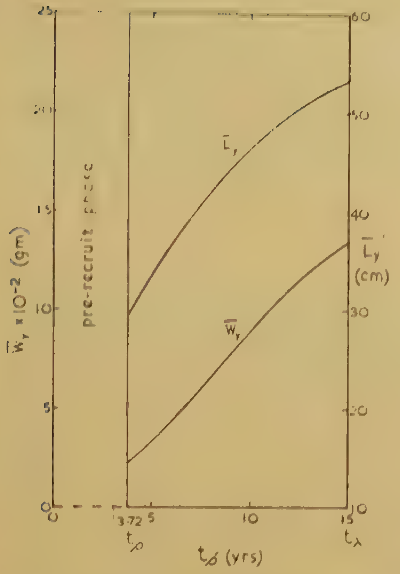

FIG. 17.10 PLAICE:
MEAN WEIGHT AND LENGTH AGAINST MESH, PRE-WAR FISHING INTENSITY

[Mean weight, $\bar{W}_Y$, and length, $\bar{L}_Y$, of fish in the catch as functions of $t_{\rho'}$ with $F = 0.73$.]

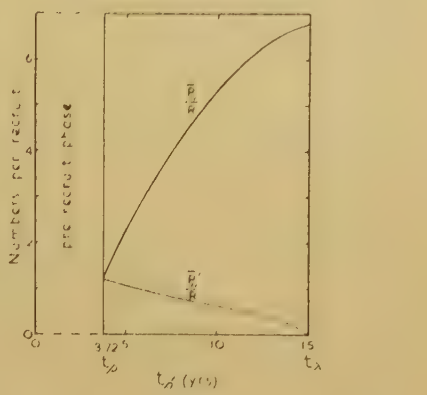

FIG. 17.11 PLAICE: POPULATION SIZE AGAINST MESH, PRE-WAR FISHING INTENSITY

[Population numbers per recruit of the exploited phase, $\bar{P}'_N/R$, and total numbers, $\bar{P}_N/R$, as functions of $t_{\rho'}$ with $F = 0.73$.]

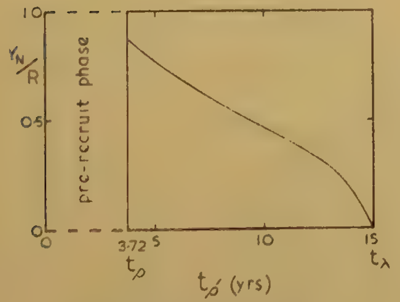

FIG. 17.12 PLAICE:
YIELD IN NUMBER AGAINST MESH, PRE-WAR FISHING INTENSITY

[Yield in number per recruit, Y_N/R, as a function of $t_{\rho'}$ with $F = 0.73$.]

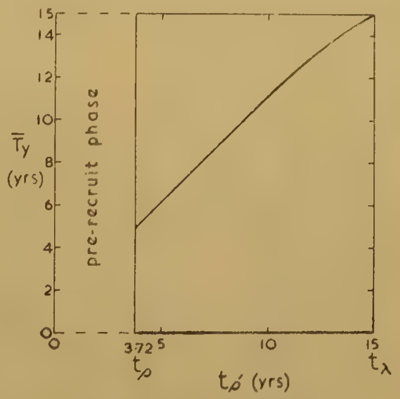

FIG. 17.13 PLAICE:
MEAN AGE OF FISH AGAINST MESH, PRE-WAR FISHING INTENSITY

[Mean age of fish in catch and exploited phase, $\bar{T}_Y$, as a function of $t_{\rho'}$ with $F = 0.73$.]

Fig. 17.14 shows isopleths of annual yield in weight per recruit, i.e. Y_W/R as a function of F and $t_{\rho'}$. The curves of Figs. 17.2 and 17.8 are represented on isopleth diagrams of yield by longitudinal or transverse sections at the appropriate values of $t_{\rho'}$ or F respectively; thus in Fig. 17.14 the horizontal line at $t_{\rho'} = 3.72$ indicates the section corresponding to the curve of Fig. 17.2, and the vertical dotted line at $F = 0.73$ that corresponding to the curve of Fig. 17.8. The pre-war values in the plaice of $F = 0.73$ and $t_{\rho'} = 3.72$ give the point on the diagram indicated by P. Sections taken parallel to the F-axis at various levels of $t_{\rho'}$ show that $(F)_{\max}$ increases as $t_{\rho'}$ increases, and that the curves of yield with respect to F at these higher values of $t_{\rho'}$ become flatter; the maxima eventually disappear altogether. The change of $(F)_{\max}$ with $t_{\rho'}$ is shown approximately by the dotted line AA′. Sections parallel to the $t_{\rho'}$—axis on the other hand, show that Y_W/R first increases and then decreases at all except extremely small values of F; the value of $(t_{\rho'})_{\max}$ increases with F, as does $(F)_{\max}$ with $t_{\rho'}$. The course of this increase is indicated by the upper dotted curve BB′. The maximum possible value of Y_W/R is seen from this diagram to be at $F = \infty$ corresponding to a value of $t_{\rho'} = 13.35$ years. This is the age at which (with the simple population model) the total weight of a year-brood is at its greatest, and this depends on the balance between decrease in numbers through natural mortality and increase in weight of the survivors.

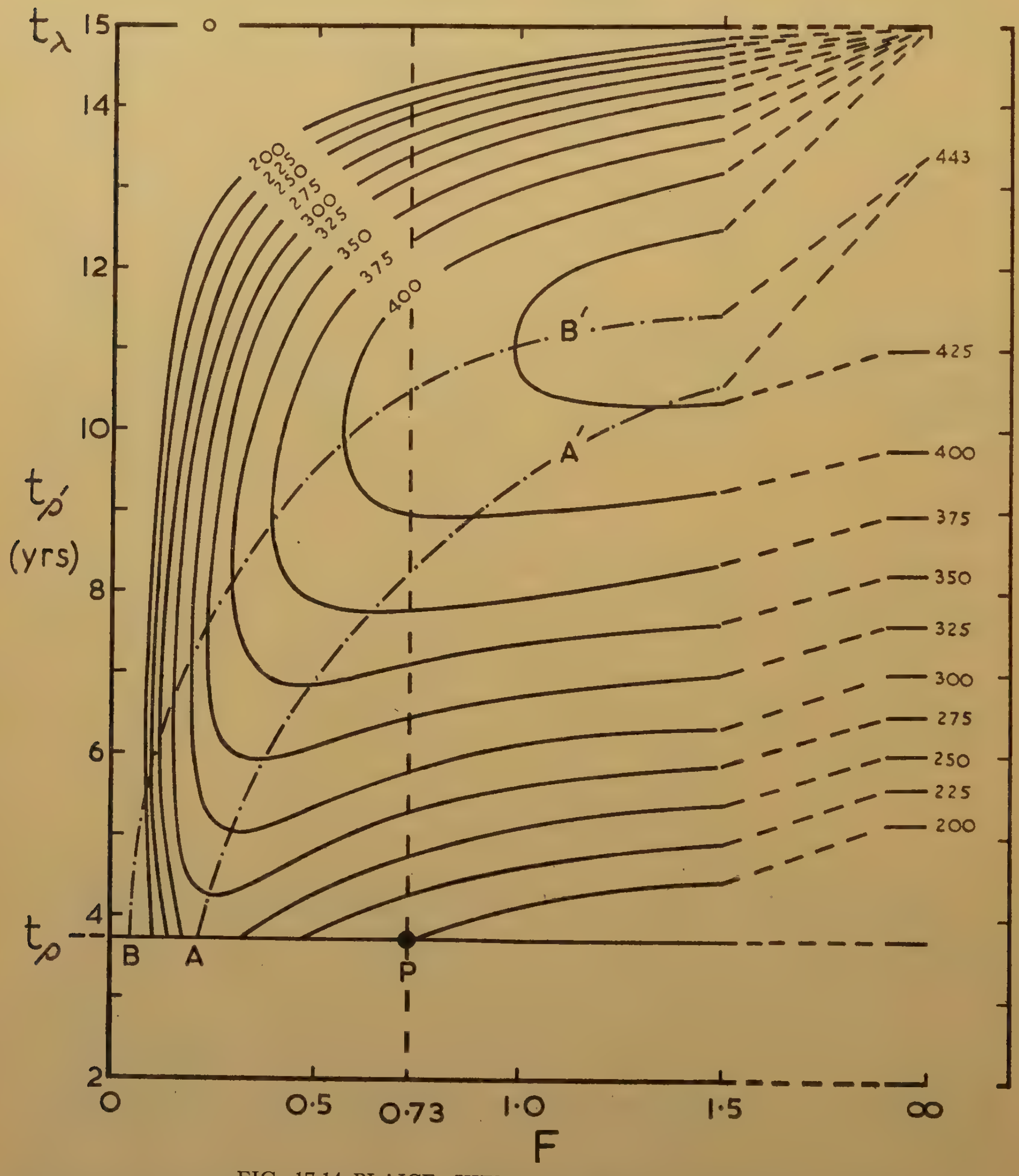

FIG. 17.14 PLAICE: YIELD ISOPLETH DIAGRAM

[This shows the steady yield obtained from any combination of F and $t_{\rho'}$. Contours are of yield per recruit at intervals of 25 gm. The top and left hand borders of the diagram are the zero contour of Y_W/R. The line AA′ joins the maxima of yield-mortality curves (e.g. Fig. 17.2), while the line BB′ joins the maxima of yield—mesh curves (e.g. Fig. 17.8). The point P indicates the pre-war values of F and $t_{\rho'}$.]

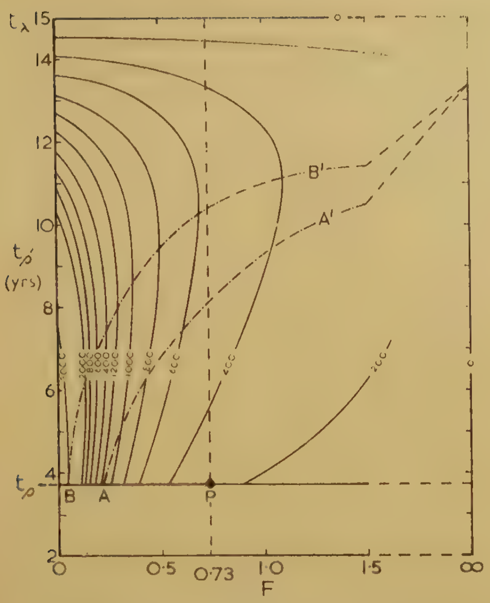

FIG. 17.15 PLAICE:
ISOPLETH DIAGRAM FOR BIOMASS OF EXPLOITED PHASE

[Contours are of $\bar{P}'_W/R$ (proportional to catch per unit effort) at intervals of 200 gm. (except the highest). The top and right-hand borders of the diagram are the zero contour of $\bar{P}'_W/R$. The lines AA′ and BB′ are drawn from Fig. 17.14, and the point P indicates the pre-war values of F and $t_{\rho'}$.]

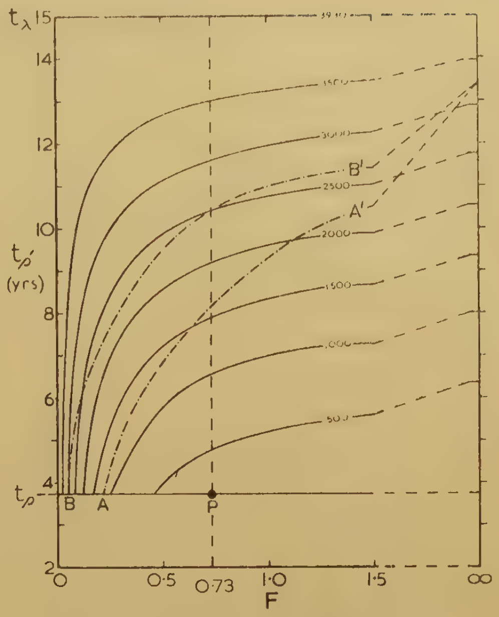

FIG. 17.16 PLAICE:
ISOPLETH DIAGRAM FOR TOTAL BIOMASS

[Contours are of $\bar{P}_W/R$ at intervals of 500 gm. The top and left hand borders of the diagram are the contour for maximum possible biomass, i.e. in the virgin stock. The lines AA′ and BB′ are drawn from Fig. 17.14, and the point P indicates the pre-war values of F and $t_{\rho'}$.]

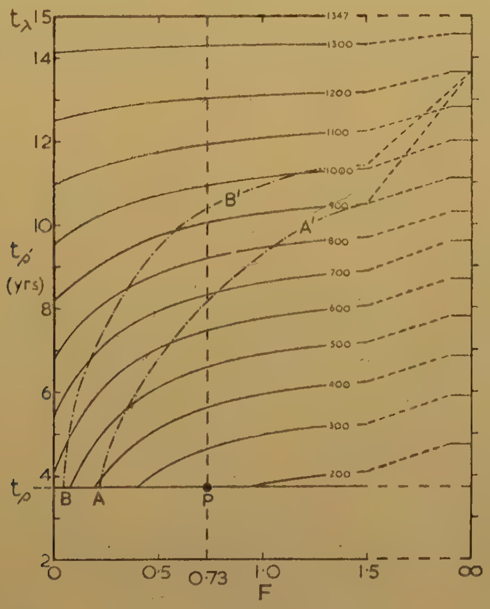

FIG. 17.17 PLAICE:
ISOPLETH DIAGRAM FOR MEAN WEIGHT OF FISH IN THE CATCH

[Contours of $\bar{W}_Y$ at intervals of 100 gm. The top border of the diagram is the contour for the average weight of a fish 15 years old. The lines AA′ and BB′ are drawn from Fig. 17.14 and the point P indicates the pre-war values of F and $t_{\rho'}$.]

We shall need to consider yield isopleth diagrams again when discussing fishery regulation in §19.1. For the moment we simply point out the important conclusion that it seems possible to obtain values of yield near the asymptote only by using large enough values of both fishing intensity *and* mesh size. Evidently, both these factors must be regarded as completely complementary in their effect, and of equal importance in describing the characteristics of fishing activity and in deciding the best regulatory methods to be used. Attention is also drawn to the points corresponding to the pre-war values of F and $t_{\rho'}$; it appears that there exists a wide range of combinations of values of fishing intensity and mesh size which could have produced a greater yield.

Isopleths of $\bar{P}'_W/R$ are shown in Fig. 17.15, sections through which at the appropriate values of F and $t_{\rho'}$ are to be related to Figs. 17.3 and 17.9 respectively. The dotted lines AA′ and BB′ correspond to those appearing in Fig. 17.14, and, as before, the pre-war values of F and $t_{\rho'}$ are indicated by the point P. It will be noticed firstly that $\bar{P}'_W/R$ decreases with F at all values of $t_{\rho'}$, though this decrease is least when $t_{\rho'}$ is large. The variation of $\bar{P}'_W/R$ with respect to $t_{\rho'}$ depends, however, on the particular fishing mortality that is postulated. Thus at low values of F, $\bar{P}'_W/R$ decreases continuously as $t_{\rho'}$ increases, but at higher values of F a maximum appears. From these diagrams we can therefore see that reductions in fishing intensity, except when the mesh is very large, are likely to result in more pronounced increases in catch per unit effort than would be obtained by increases in mesh size. At very low fishing intensities an increase in mesh size might even cause a reduction in catch per unit effort, though it will be noted that the pre-war position is very far removed from that part of the diagram where such an effect appears, and any increase in mesh size or decrease in fishing intensity from the pre-war condition would appear to have a beneficial effect on the catch per unit effort.

Two other isopleth diagrams that we have reproduced are those of $\bar{P}_W/R$ and $\bar{W}_Y$, in Figs. 17.16 and 17.17 respectively. The behaviour of both these population characteristics is relatively simple: they increase as F decreases and $t_{\rho'}$ increases. As before, the lines AA′ and BB′ correspond to those of Fig. 17.14, and the pre-war state is indicated by the point P.

We shall see later, in §19.1.1, how isopleth diagrams form the essential basis for a consideration of the general principles involved in the regulation of a fishery. For the remainder of this section, however, we investigate the effects of particular parameters in determining the shapes of the curves of population characteristics plotted against F or $t_{\rho'}$ separately, and attempt to assess the influence of possible errors in the values of parameters that we have used for plaice.

17.5 THE INFLUENCE OF PARTICULAR PARAMETERS ON THE YIELD CURVE

17.5.1 *Natural mortality* (M)

The parameter that is of the greatest importance in this connection is perhaps the *natural mortality*, M. Not only is its determination from data often difficult, but as we shall see, variation in its magnitude can have important influences on the shape of the curves of Y_W/R. Fig. 17.18.1 shows curves of Y_W/R as a function of F in which M has values of 50% above and below those hitherto used, the values of all other parameters being the same as for Fig. 17.2. This range of M may be taken as a possible range within which the annual mean natural mortality might well lie. It will be seen that the curves with $M = 0.05$ and 0.15 have the same general shape as that for $M = 0.10$, but as M increases there is a marked decrease in $(Y_W/R)_{\max}$ and an appreciable increase in the corresponding value of $(F)_{\max}$. Eventually, with high enough values of M, the maximum in the yield curve no longer occurs within the working range of F and may disappear altogether, as can be seen from the additional curve with $M = 0.5$, shown as a broken line. Clearly, these kinds of changes in shape of yield curves have an important bearing on the question of how a population will react to various amounts of fishing. Because of their tendency to increase $(F)_{\max}$, the effect of values of M greater than 0.1 in plaice is particularly relevant, though

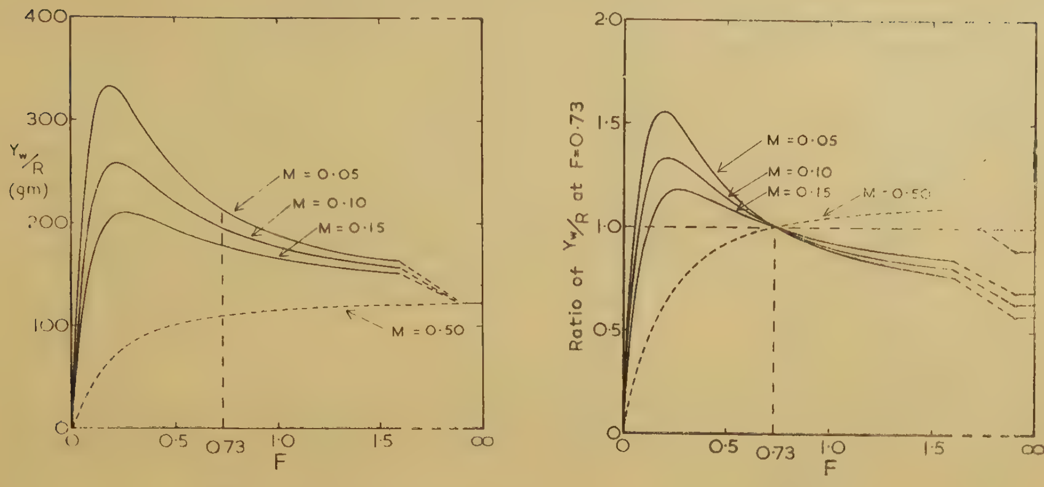

Fig. 17.18.1 Fig. 17.18.2

FIGS. 17.18 PLAICE: EFFECT OF DIFFERENT NATURAL MORTALITIES ON YIELD-FISHING MORTALITY CURVES

[Yield per recruit, Y_W/R, as a function of F with $t_{\rho'} = 3.72$ yrs., taking $M = 0.05$,.1, 0 0.15 and 0.5 respectively.]

Fig. 17.18.1 Curves of Y_W/R as calculated from (4.4).

Fig. 17.18.2 Curves of Y_W/R adjusted to unity at $F = 0.73$, to show effect of values of M other than 0.1 on predictions of changes in yield with fishing mortality relative to pre-war conditions.

it will be seen that even with $M = 0.15$, $(F)_{\max}$ is still less than half the pre-war fishing mortality.

Now, for assessing the errors that might be involved in predictions of yield based on an incorrect estimate of M, what matters is the distortion in the shape of the calculated yield curve relative to the true curve. This is because predictions will almost always be of the relative change in yield from an observed level that would be expected to result from a proposed change in either F or $t_{\rho'}$. In the present case we are taking the average conditions during the years 1930-1938 as reference; hence the range of error that might be involved if the true value of M were not 0.1 but lay between 0.05 and 0.50 is best estimated by transforming the curves of Fig. 17.18.1 to give unit yield at the pre-war value of $F = 0.73$. This procedure, the results of which are shown in Fig. 17.18.2, does not alter the shape of the curves or the positions of $(F)_{\max}$, but shows immediately, for any given value of F, the different estimates of yield that would be obtained if other values of M were effective, as a proportion of the pre-war yield.

We now consider the effect of the magnitude of M on curves of Y_W/R against $t_{\rho'}$ (Fig. 17.19.1), taking the same range of M as before. It will be noted that the level of the curves and the value of $(t_{\rho'})_{\max}$ are decreased as M increases. Again, therefore, we have to beware of underestimating the value of M. Estimates of the relative change in yield corresponding to a given value of $t_{\rho'}$ using values of M other than the central value of 0.1 are again best compared by reducing the curves of Fig. 17.19.1 to unity at the pre-war value of $t_{\rho'}$, i.e. 3.72 years. The resulting curves are shown in Fig. 17.19.2.

17.5.2 *Length of life* (t_λ)

We next consider the effects of taking different values of t_λ, the age at which fish reach the end of their fishable life-span. It will be remembered that t_λ is to some extent arbitrary, since we have no evidence to suggest that plaice do, in fact, die immediately they reach a certain age. On the other hand, data for determining values of other parameters for fish at these high ages are always scanty, particularly for the most relevant of all, the natural mortality coefficient, and this fact led us, in §13.3, to take as high a value for t_λ as was compatible with the estimation of other parameters with sufficient accuracy. Here, therefore, we need concern ourselves only with the effect of values of t_λ greater than that which we have used hitherto, i.e. 15 years.

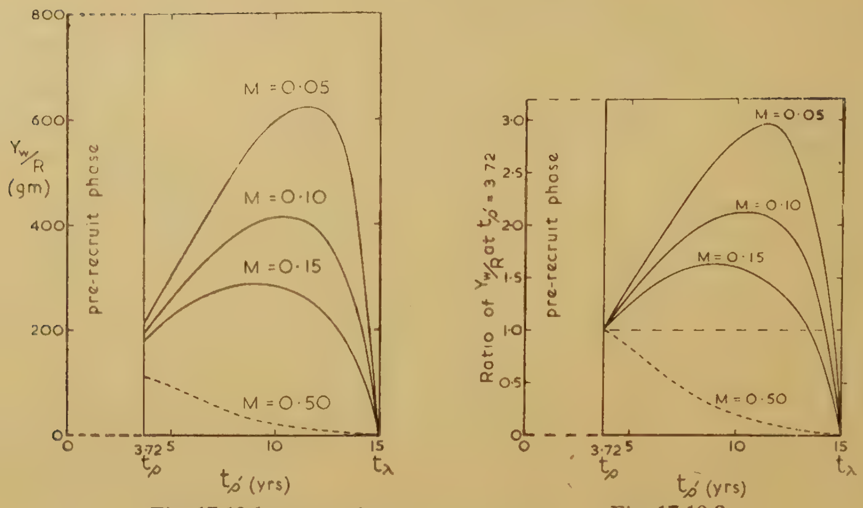

Fig. 17.19.1 Fig. 17.19.2

FIGS. 17.19 PLAICE: EFFECT OF DIFFERENT NATURAL MORTALITIES ON YIELD-MESH CURVES

[Yield per recruit, Y_W/R, as a function of t_ρ' with $F = 0.73$, taking $M = 0.05$, 0.1, 0.15 and 0.5 respectively.
Fig. 17.19.1 Curves of Y_W/R as calculated from (4.4).
Fig. 17.19.2 Curves of Y_W/R adjusted to unity at $t_\rho' = 3.72$ yrs. to show effect of values of M other than 0.1 on predictions of changes in yield with mesh relative to pre-war conditions.]

Fig. 17.20 shows curves of Y_W/R as a function of F with $t_\lambda = 15$, 18 and ∞ (years). Eighteen years may be regarded as a possible value which might have been taken if fuller data had been available, since plaice of this age do occasionally occur in samples; while putting $t_\lambda = \infty$ produces the most extreme effect possible. The equations for yield derived by Baranov (1918) and Ricker (1944) have, in effect, $t_\lambda = \infty$ (see §17.8). The effect of an increase in t_λ is in general to decrease $(F)_{\max}$ and increase $(Y_W/R)_{\max}$, but above $F = 0.5$ the value of Y_W/R for the plaice is virtually the same for all values of t_λ greater than 15. We can therefore say that predictions of the higher yield to be expected from values of F

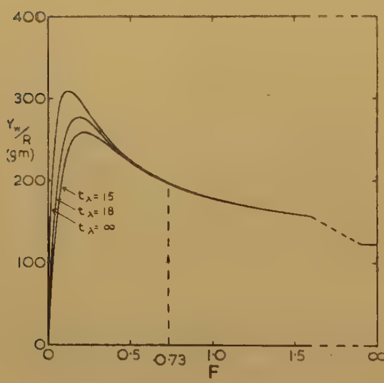

FIG. 17.20 PLAICE: EFFECT OF DIFFERENT VALUES OF MAXIMUM AGE ON YIELD-FISHING MORTALITY CURVES

[Yield per recruit, Y_W/R, as a function of F with $t_\rho' = 3.72$ yrs. taking $t_\lambda = 15$, 18 and ∞ yrs. respectively.]

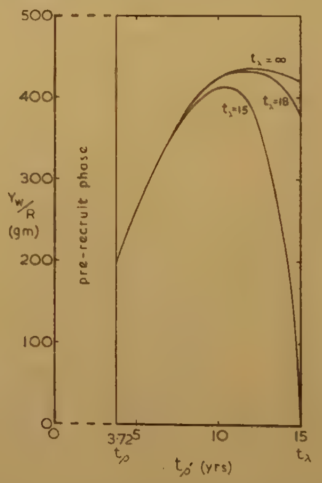

FIG. 17.21 PLAICE: EFFECT OF DIFFERENT VALUES OF MAXIMUM AGE ON YIELD-MESH CURVES

[Yield per recruit, Y_W/R, as a function of t_ρ' with $F = 0.73$, taking $t_\lambda = 15$, 18 and ∞ yrs. respectively.]

lower than the pre-war figure are not likely to be greatly in error if the value of t_λ we are using should prove to be too small. Furthermore, such predictions would tend to underestimate the advantage of reducing the fishing mortality and thus, in making them, proper caution would be exercised.

Turning now to the effect of these higher values of t_λ on the behaviour of Y_W/R with changes in $t_{\rho'}$ (Fig. 17.21), we find, as mentioned earlier, that at very high values of $t_{\rho'}$ it is considerable. The effect is only noticeable, however, above a value of $t_{\rho'}$ of about 8 years (corresponding in plaice to a mesh of the order of 160 mm.), and is still of minor importance at $(t_{\rho'})_{\max}$. Within the range of $t_{\rho'}$ likely to been encountered we can certainly say that the use of values of t_λ higher than 15 for plaice would produce no appreciable effect on predictions of Y_W/R.

17.5.3 *Growth* (K *and* W$_\infty$)

Growth parameters are perhaps the easiest to estimate accurately, and the question of errors in them will usually be of minor importance. On the other hand, growth is readily influenced by environmental conditions, and we must consider briefly the effects that changes in certain of these conditions might have on the reaction of a population to exploitation, as a result of their effect on the growth of its individuals.

The two main parameters of the von Bertalanffy growth equation are K and W_∞ (§9.4.2), the former being proportional to the coefficient of catabolism and the latter to the cube of the ratio of the coefficients of anabolism and catabolism. Changes in an environmental factor such as temperature that influence the general rate of metabolism can reasonably be assumed in poikilothermic animals to affect the coefficients of both anabolism and catabolism to roughly the same extent. Hence the effect of different temperatures on growth can be represented to a first approximation by keeping W_∞ constant but varying K, possibly in accordance with van't Hoff's law. Large changes in K have to be made before noticeable differences in the shape of yield curves are caused, and in Fig. 17.22 are shown curves of Y_W/R for values of K roughly half (0.05) and double (0.20) the central value of 0.095, with $W_\infty = 2867$ gm. as before. It will be seen that the level of the curves differs greatly, which is due to the difference in weight of individual fish in the exploited phase that these values of K imply, as shown in the corresponding growth curves of Fig. 17.23. Changing K in this way implies corresponding changes in the coefficient of anabolism E such that the limiting weight W_∞ remains constant. At any lower weight,

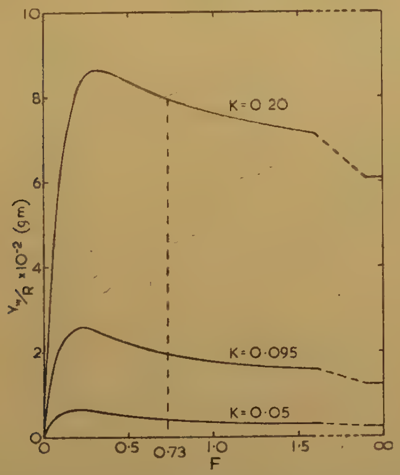

FIG. 17.22 PLAICE: EFFECT OF DIFFERENT GROWTH RATES ON YIELD-FISHING MORTALITY CURVES

[Yield per recruit, Y_W/R, as a function of F with $t_{\rho'} = 3.72$ yrs. taking $K = 0.05$, 0.095 and 0.20 respectively.]

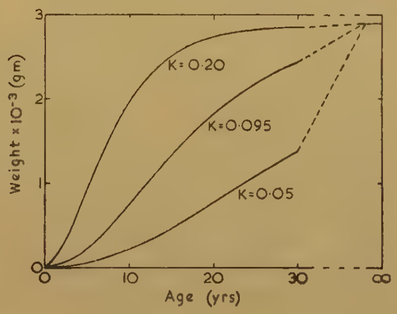

FIG. 17.23 PLAICE: CURVES OF GROWTH IN WEIGHT GIVEN BY THE VALUES OF K USED IN FIG. 17.22

[In each case W_∞ and t_0 have their usual values, i.e. 2867 gm. and –0.815 yrs. respectively.]

anabolism is thus decreased relatively less than catabolism since the former is a function of the two-third power of body weight while the latter is a function of body weight itself. It is interesting to note that D. H. Thompson (1941) has concluded from other evidence that the differences in temperature of certain American lakes between latitudes 30°N. and 45°N. should result in a sixfold range in the maximum yield of fish obtainable from them, the lowest yield corresponding with the lowest temperature, as would be predicted from the curves of Fig. 17.22.

The effect of the other major environmental factor influencing growth—the food supply—may be represented by appropriate changes in the rate of anabolism and hence in the magnitude of W_∞ but not of K. Inspection of equation (4.4) for yield shows that if t_0 is also constant then the yield is directly proportional to W_∞, so that changes in the value of W_∞ cannot alter the shape of yield curves. For t_0 to remain constant in these circumstances, however, would require that the change in growth applied to fish of all ages. If, as is more likely, the change is of a different magnitude in the pre- and post-recruit phases, or is restricted to the latter only, the value of t_0 will not be constant (see §18.4.1) and a change in the position of $(F)_{\max}$ would be involved. The importance of the relationship between food and growth is that it is involved when changes occur in population density due to changes in the amount of fishing, and this is dealt with more fully in §18.4.

17.6 Conclusions for Plaice

Our investigation, in this section, of the behaviour of the simple population models of Part I leads to some provisional conclusions concerning the reaction to exploitation of the North Sea plaice population. It will be remembered that these models contain parameters whose values refer to the pre-war state of that population. Consequently, their reliability for predicting the effects of various fishing intensities or cod-end mesh sizes may be expected, in general, to vary inversely with the extent to which the new values of these characteristics of fishing activity differ from those effective before the war. Particularly is this the case in so far as values of parameters used in the models are likely to vary with population density; for example, when growth is made to vary in this way there is an appreciable effect on the size of mesh that is equivalent to a given value of $t_{\rho'}$, a problem which is considered in §18.4.1. Bearing in mind these qualifications, it may be useful briefly to summarize our findings of §17 as a background against which to assess the consequences of introducing the more detailed treatments of Part II discussed in the next section and summarized in §18.8.

Dealing first with the effects of reducing fishing intensity below the pre-war level, but retaining the same cod-end mesh size then in use, it would appear that a greater sustained yield could thereby be obtained from the plaice population. Moreover, this increased yield would be obtained with a considerably higher catch per unit effort, and the average size of the fish caught would be greater. Increases in the size of the cod-end mesh, while maintaining the pre-war fishing intensity, would seem to give the same results; i.e. an increase in yield, in catch per unit effort, and in the average size of fish caught.

The potential increases in yield, catch per unit effort, and average size of fish become particularly pronounced when the effects of simultaneous changes in fishing intensity and cod-end mesh size are considered. Thus, from Figs. 17.14, 17.15 and 17.16 it would appear that there exists a wide range of combinations of values of fishing intensity and cod-end mesh size that would produce values of the above catch characteristics not only higher than were obtained before the war, but also higher than it would be possible to obtain by changes in either factor alone. So it would seem that only by suitable adjustments of both fishing intensity *and* cod-end mesh size is it possible to achieve the greatest efficiency of exploitation—a conclusion which we show later (§19.1) to hold good in all circumstances and to be of great importance in fishery regulation.

In §17.5 we investigated the consequences of possible errors in the values of certain parameters which had been used hitherto, though in no case did we find that any of our conclusions were qualitatively changed as a result. Of these parameters, the natural mortality coefficient needs special mention as probably the one that can have the most critical effect on the predicted reaction of a population to exploitation (see, e.g. Kesteven, 1950).

It will be noted that all these conclusions follow from a study of theoretical models in which population characteristics are expressed in the units 'per recruit', and are in no way altered if absolute units are used. The main variables Y_W/R and F may, however, readily be expressed in practical units as follows. We gave in §15.2.1 an estimate of the mean annual recruitment in North Sea plaice of 2.8×10^8, so that annual yield in absolute units is given as

$$Y_W = 2.8 \times 10^8 \times \frac{Y_W}{R} \ (gm.)$$

An estimate of the factor, c, for converting fishing mortality coefficient to fishing intensity in the plaice fishery, has already been given in §14.1.3.1, viz.:

$$F = 0.25 f$$

where f is expressed in the units 'thousands of steam-trawler ton-hours fishing per square nautical mile per year'. As time passes, changes in the efficiency of vessels, gear and fishing methods will alter the value of c unless a particular type of ship and gear is taken as a permanent standard of reference (see §12.4).

A relationship between $t_{\rho'}$ and cod-end mesh size for plaice can be obtained from Fig. 15.13 but, as mentioned before, this assumes that growth does not vary with density. When dealing with cases when this assumption is no longer acceptable (e.g. §18.4), it will be necessary to compute the behaviour of yield with respect to changes in mesh size itself.

17.7 BRIEF DISCUSSION OF APPLICATION TO THE HADDOCK

To provide the necessary introduction to the investigation of the more complex population models in §18, we conclude by reviewing briefly the salient features of the behaviour of the simple models of Part I using parameter values for North Sea haddock determined in Part III. We have found no fundamental differences between the predicted behaviour of plaice and haddock, and we shall illustrate for haddock only those relationships to which specific reference is made later in Part IV, or which have no counterpart in plaice.

Fig. 17.24 shows the annual yield in weight per recruit, Y_W/R, as a function of F, computed from (4.4) using the parameter values for the pre-war state of the haddock

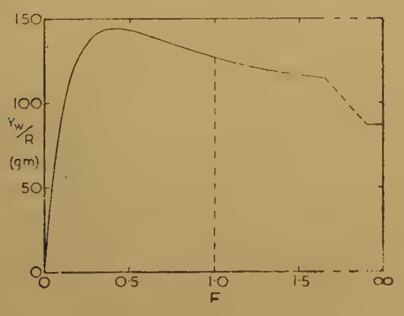

FIG. 17.24 HADDOCK: YIELD AGAINST FISHING MORTALITY, 70 MM. MESH

[Yield per recruit, Y_W/R, as a function of F with $t_{\rho'} = 1.83$ yrs. Vertical broken line shows pre-war fishing mortality ($F = 1.0$). The remaining parameters used to construct this and other haddock diagrams of §17 are as follows: $M = 0.20$, $W_\infty = 1209$ gm., $K = 0.20$, $t_0 = -1.066$ yrs., $t_\rho = 1$ yr., $t_\lambda = 10$ yrs.]

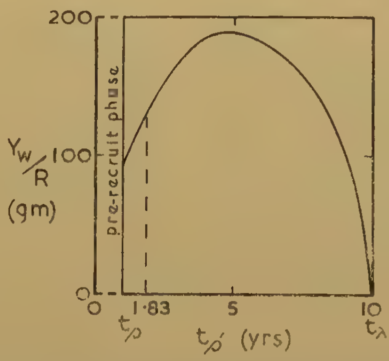

FIG. 17.25 HADDOCK: YIELD AGAINST MESH, PRE-WAR FISHING INTENSITY

[Yield per recruit, Y_W/R, as a function of $t_{\rho'}$ with $F = 1.0$. Vertical broken line is at pre-war mesh (taken as 70 mm.).]

population which are listed in the figure legend. It will be seen that the shape of the curve is similar to the corresponding curve for plaice shown in Fig. 17.2, and, in particular, it has a maximum at a value of F again about one-third of the pre-war value—indicated by the broken line. The variation of Y_W/R with respect to $t_{\rho'}$, holding F constant at 1.0, is shown in Fig. 17.25, and again the general similarity to plaice (Fig. 17.8) is apparent. The broken line indicates the pre-war value of $t_{\rho'}$.

The more general behaviour of yield in haddock is seen from the isopleths of Y_W/R shown in Fig. 17.26, where the values for F and $t_{\rho'}$ which we are taking to refer to the pre-war state are indicated by the point H. As in plaice (Fig. 17.14), it would appear that there is a wide range of combinations of values of fishing intensity and cod-end mesh size that would give a higher sustained yield.

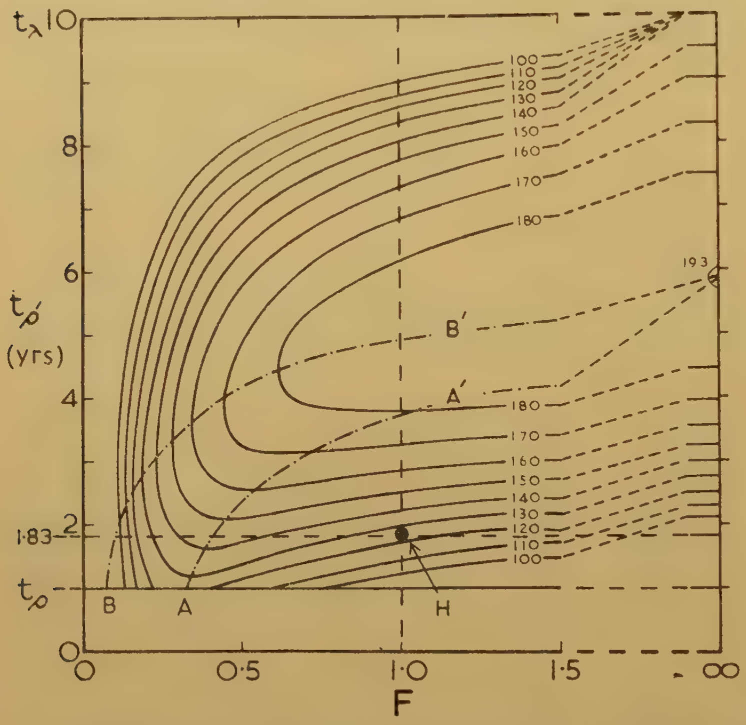

FIG. 17.26
HADDOCK:
YIELD ISOPLETH
DIAGRAM

[Isopleths of Y_W/R at intervals of 10 gm. The top and left-hand borders are the zero isopleth of Y_W/R. As in Fig. 17.14, the lines AA′ and BB′ are drawn through the maxima of the yield-fishing mortality and yield-mesh curves respectively, and the point H indicates the pre-war values of F and $t_{\rho'}$.]

Of the remaining population characteristics we need mention here only the annual mean biomass of the exploited phase and of the whole post-recruit phase, $\bar{P}'_W/R$ and $\bar{P}_W/R$ respectively, expressed as functions of F. These are of special interest here because in plaice they are identical owing to the high age at recruitment in that species. Curves of $\bar{P}_W/R$ and $\bar{P}_W/R$ for haddock are shown in Fig. 17.27 and it will be seen that the curve of $\bar{P}_W/R$ is higher at $F = 0$ than that of $\bar{P}'_W/R$, and, as $F \to \infty$, tends to a positive asymptote which is the biomass of the pre-exploited phase. The curve of $\bar{P}'_W/R$, on the other hand, tends to zero as $F \to \infty$.

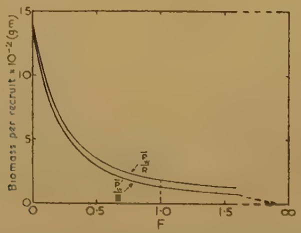

FIG. 17.27 HADDOCK:
BIOMASS AGAINST FISHING MORTALITY,
70 MM. MESH

[Biomass per recruit of exploited phase, $\bar{P}'_W/R$ (proportional to catch per unit effort) and total biomass per recruit, $\bar{P}_W/R$, as functions of F with $t_{\rho'}$ = 1.83 yrs.]

Isopleths of $\bar{P}'_W/R$ are shown in Fig. 17.28, and it will be seen that values are generally lower than in plaice (Fig. 17.15). Since $\bar{P}'_W/R$ is proportional to catch per unit effort it would seem that the haddock is less productive per recruit than the plaice, and we may note in this connection that the weight-at-age is lower, and the value of M we are using is higher, than in plaice. The fact that the actual yield of haddock is greater than that of plaice is due to the greater recruitment in the former species (see §15.2.1).

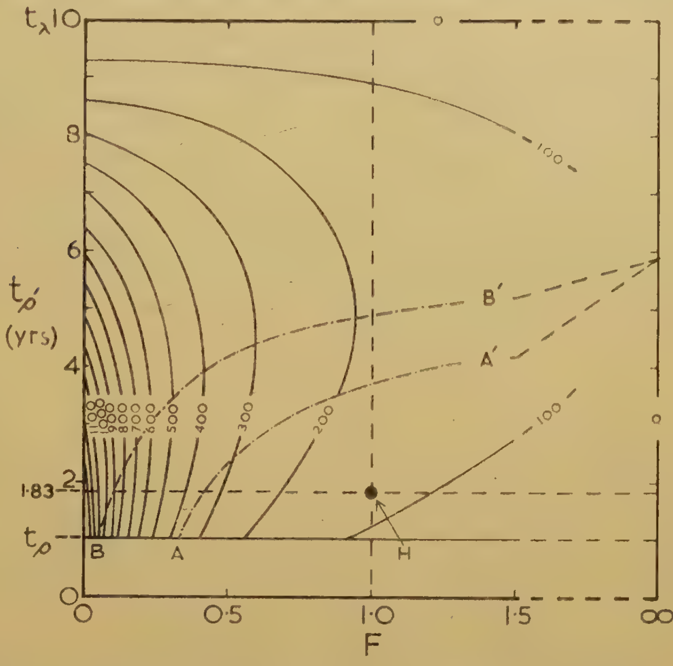

FIG. 17.28 HADDOCK: ISOPLETH DIAGRAM FOR BIOMASS OF EXPLOITED PHASE

[Contours are of $\bar{P}'_W/R$ (proportional to catch per unit effort) at intervals of 100 gm. The top and right hand borders are the zero contour of $\bar{P}'_W/R$. Lines AA′ and BB′ are drawn from Fig. 17.26 and the point H indicates the pre-war values of F and t_ρ'.]

As far as can be judged from the behaviour of the simple population models our conclusions for plaice summarised in §17.6 apply also to haddock.

17.8 REVIEW OF PUBLISHED THEORETICAL MODELS

In Part II we referred briefly to certain aspects of the theoretical methods used by previous authors. Having examined the properties of our simple models it is convenient at this stage to discuss more fully the theoretical models of an exploited fish population that have been developed by other workers, since all but one* involve the assumption that the parameters of recruitment, growth and natural mortality are constant, and are therefore directly comparable with our own treatment in Part I. In this review of literature we are concerned primarily with an analysis of the theoretical methods that have been adopted by other authors; the bearing of conclusions drawn from them on problems of fishery regulation are discussed, where relevant, in §19.1.6.

Baranov (1918) was the first to develop a theoretical model of an exploited fish population. He postulated that fishing and natural mortality rates could be represented by means of instantaneous coefficients, as we have done in Part I. Baranov also assumed, in effect, that recruitment takes place continuously throughout the year which, as we mentioned in §8.3.1, leads to identical equations defining the steady state but is not a convenient procedure when it becomes necessary to identify individual age-groups. It is in the mathematical representation of growth that his treatment differs essentially from our own. Thus Baranov, who was also dealing with plaice, assumed that the length of a fish was proportional to its age; as can be seen from the growth in length data for this species shown in Fig. 16.7, this could be a reasonable approximation over a limited range of age. However, to obtain the total yield from the population Baranov integrated from the length at which fish enter the exploited phase to infinity. Since he also converted length to weight by a cubic expression his procedure involves extrapolating to an infinite age a growth function that is not asymptotic. For this reason we may suspect that the resulting population model would be unreliable, especially at low values of the fishing mortality coefficient. The general behaviour of the model represented by Baranov's equation 8 is summarised graphically in his Fig. 10, which shows the yield per gm.-recruit as a function of the fishing mortality coefficient (k_2) for various values of the natural mortality coefficient (k_0). To give some idea of the differences between it and our model we show in Fig. 17.29 the yield according to each, as a function of the fishing mortality coefficient. Curve (b) is obtained by Baranov's method, with (k_0) = 0.021 (which is equivalent to a value of $M = 0.1$) and a length at entry to the exploited phase of 30 cm. The ordinates are transformed to give unit yield at $F = 0.73$. Curve (a) is obtained from (4.4) with $t_\rho = 5.286$ years (to correspond with length at first capture of 30 cm.) and $t_\lambda = \infty$, and is transformed in the same way. The two curves have some general similarity and Baranov arrived at what we believe to be a correct appreciation of the behaviour of an exploited fish stock from a study of his theoretical model; nevertheless serious errors would be incurred in attempting to predict by it the yield at low fishing intensities.

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*This is the equation published by Doi (1951) in which year to year variations in recruitment are allowed for. It has been referred to in §6.2.

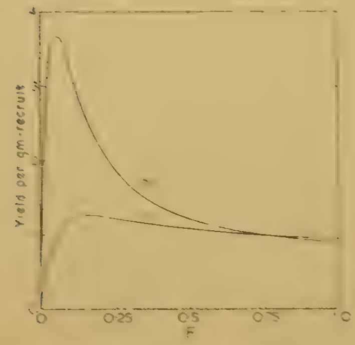


FIG. 17.29 PLAICE: COMPARISON WITH BARANOV'S YIELD CURVE

[Yield per gm.-recruit as a function of F using Baranov's equation, curve (b), and (4.4), curve (a). The much higher maximum in Baranov's curve is due to the particular growth equation he used (see text).

Recently, a modification of Baranov's treatment has been published by Yoshihara (1951), who represents growth in length by the logistic equation. Because this gives an asymptotic curve this procedure avoids the main objection to Baranov's; the limitation of Yoshihara's method is that curves of growth in length of fish are not symmetrical sigmoids, and only lengths greater than half the asymptotic length could be represented adequately by the logistic equation.

The fact that Baranov treats the population as a length, rather than as an age, distribution means that the rate of growth does not appear in his equation as such; it is therefore not a suitable starting point for the study of more complex phenomena such as the variation of growth with density. This difficulty is avoided by Yoshihara's method, and also in the population model developed by Silliman (1945) for estimating the total mortality coefficient from a knowledge only of the length distribution of the population. This is otherwise similar to Baranov's in many respects, but employs a polynomial of the third power to relate length and age. This gives a curve which is convex at first but at higher ages passes through an inflection and then ascends as does a simple cubic. It gives a good fit within the range of the data, but as it is integrated to an infinite age in Silliman's model there is the possibility that the latter will tend to overestimate the average weight of fish in the catch (and also yield, if used for that purpose) at low fishing intensities.

Thompson and Bell (1934) used percentage rates to represent fishing and natural mortality, which leads to the same results as the use of instantaneous coefficients. They also treat weight as increasing by a constant percentage in each year of life, so that growth is represented in the same way as natural and fishing mortality, and this geometrical increase can be regarded as an approximate expression of exponential growth. This assumption was based on weight-at-age data for the Pacific halibut covering a limited range of age, over which it is possible to fit a simple exponential expression, but as mentioned in §9.1, the implications of assuming that this pattern of growth would continue throughout life are untenable. The particular representation of growth used by Thompson and Bell is responsible for the features of the yield curves shown in their Fig. 9, where with a low natural mortality rate the yield reaches enormously high values as fishing mortality is decreased. These authors recognised the anomaly of this, but supposed that in practice the natural mortality rate would increase so as to compensate for the reduced fishing mortality rate. However, it is really due to the fact that with the high survival permitted at low fishing intensities, the total weight of older fish has become inordinately large through assuming that growth proceeds at a constant percentage rate.

Ricker (1944) and Doi (1951) have both expressed growth and mortality as simple exponential functions, although the latter author also uses a linear equation as an alternative. They therefore make essentially the same assumption as Thompson and Bell, but these are expressed in more formal mathematical terms. Doi places an upper limit to the life-span for purposes of integration and thus avoids the errors involved in Thompson and Bell's method. Ricker, by supposing that the life-span is of infinite duration, obtains the equation for yield:—

$$Y = \frac{Wp}{p + q - k} \quad \ldots \quad (17.1) \equiv 34 \text{ of Ricker}$$

where p, q and k are the coefficients of fishing mortality, natural mortality and growth respectively, and W is the total weight of each year-brood of recruits. In this equation p and q are identical with our F and M, while W can be written in our terminology as $Rw_{\rho'}$, R being the annual number of recruits and $w_{\rho'}$ the average weight of each. Referring to (17.1) it will be seen that if $q > k$, then at all values of p there is a positive yield which approaches an asymptote as $p \to \infty$. In these circumstances (17.1) is formally identical with (5.9) for yield in numbers with $\lambda = \infty$. When $q = k$, the yield is simply the initial weight of all the recruits, W, and is therefore constant for all values of p. Finally, when $q < k$, the yield is infinitely large when $p \leqslant (k - q)$ and finite only when $p > (k - q)$. Some of these properties are shown in Ricker's Fig. 1.

We therefore find that the main difference between the theoretical models of Part I and those developed by all the above authors lies in the representation of growth, and that the method used by Thompson and Bell, especially when given a rigorous formulation as in Ricker's equation, may sometimes lead to predictions that are not acceptable even as a first approximation. Another—not unimportant—difference is that in none of the models mentioned above is entry to the exploited area at age t_ρ, i.e. the age at recruitment as we define it (see §3.1), distinguished from entry to the exploited phase at age $t_{\rho'}$. As a result they cannot be used, as they stand, to investigate or predict the effects of changes in size of mesh, or second order effects restricted to the post-recruit phase such as that of density on growth (except in the special case of $t_\rho = t_{\rho'}$).

There are a number of other papers in which theoretical population models have been developed; some of these are concerned primarily with methods of estimating parameters (De Lury, 1947; Ricker, 1948) and are referred to where appropriate in Part III, while others such as those of Thompson (1937) and Ricker (1940) deal only with mortality rates, using the same methods as those discussed above. The approach adopted by Kesteven (1946), on the other hand, differs from all others in that he represents mortalities by decrements which do not depend on the number of fish present. This method would seem incompatible with what is known about mortality in most exploited fish populations, and must be regarded as being applicable to special cases only (see §8.3.2).

Hitherto, we have been concerned with methods which may be regarded as analytical in character, in that the separate processes underlying the behaviour of a population are distinguished, and represented mathematically; these formulations are then combined to produce a theoretical model of the population. A method that is not analytical is the 'sigmoid curve' theory, developed by Hjort, Jahn and Ottestad (1933) and Graham (1935, 1939) and subsequently adopted in essence by a number of other authors in discussing problems of fishery exploitation (e.g. Sette, 1943b, Baerends, 1947 and Schaefer, 1954 a, b). This starts from the concept of the sigmoid growth of a population, and assumes that the total weight of a fish population would increase in this way in the natural state. This being so, the population would be increasing at the maximum rate when its abundance reached a value corresponding to the inflection of the sigmoid growth curve, and it is then postulated that if the fishing mortality could be adjusted so as to remove each year exactly this amount of growth, the greatest sustained yield would be obtained.

This kind of approach is not an alternative to analysis. It has a separate function in providing a means of estimating the order of magnitude of the maximum yield and the value of F required to produce it, when data referring to specific factors are not available, though for that reason it cannot be used to investigate the effect of changes in those factors, such as in gear selectivity. There are also certain intrinsic difficulties with the method. Thus it is necessary to assume that growth in population weight is a symmetrical sigmoid, and although this may be a useful working assumption it has to be remembered that cases in which a fair approximation to symmetry has been demonstrated, such as the experimental studies of Pearl (1930) and Gause (1934), refer to increase in numbers, not in weight. The function which has been assumed to represent growth of population weight in the sigmoid curve theory corresponds to the autocatalytic growth equation mentioned in §9.1.1, and is an analogue of the logistic 'law' of increase in numbers. The latter has itself been the subject of criticism—particularly by workers such as Sang (1950) who have studied closely the growth of laboratory cultures under conditions which depart in certain important respects from those in nature—but it seems to describe well enough the essential features of the growth towards stationary states of the very few natural populations for which suitable data are available. The simple logistic interpreted in terms of biomass implies, however, that the rate of increase of the population depends solely on its total weight and is independent of the age- and size-composition of the individuals comprising it: the population is to be regarded, in effect, as a continuous, homogeneous, mass of living matter. The sigmoid curve theory as it has been applied to fisheries depends critically on this implication, since from it follows the deduction that the greatest sustained yield is obtained when the total biomass is kept equal to that at the inflection of the growth curve, and in particular that this inflection occurs in the region of half the virgin biomass. Some further observations on these points, based on the properties of theoretical models applied to North Sea plaice, will be found in §18.4.2.6.

It is not difficult to see how, in theory, the sigmoid curve method could be elaborated to avoid both these difficulties. Thus, if enough data were available the true shape of the growth (in biomass) curve of the population in question could be established from observation; but in circumstances as favourable as this the requirements for maximum yield could probably be determined empirically without recourse to theory of any kind. Again, the logistic theory could perhaps be extended to take into account the age- and size-composition of the population and hence to afford a distinction between the properties of a growing population and one which has the same biomass but is in a steady state; but the method would then be formally equivalent to the analytical approach adopted in this paper—at least as far as its demands on data are concerned (e.g. Stanley, 1932). It is when such detailed information does not exist that the sigmoid curve theory, by making the simplest reasonable assumption about the dynamics of a population, is valuable as a means of obtaining a rough appreciation from the minimum of data. Paradoxically, it is perhaps most satisfactory when applied to the behaviour of several species at once, or even of an entire community; this is the case dealt with by Graham and Baerends, and is of course the one making most demands on the data when analysis is attempted.

SECTION 18

APPLICATION OF POPULATION MODELS OF PART II

To ascertain whether the main conclusions of §17 need modification when the more detailed treatments of Part II are introduced it will be sufficient, for the most part, to study the annual mean yield per recruit, Y_W/R, as a function of F and $t_{\rho'}$ (or mesh size in some cases), since it will then usually be possible to see at once whether any profound changes in the other characteristics of commercial importance, $\bar{P}'_W/R$ and $\bar{W}_Y$, are involved. Where this is found to be the case the matter is dealt with more fully.

18.1 Mesh Selection

In the previous section we have represented fishing mortality as a function of the age of fish in the simplest way possible, by assuming that all fish become fully available to capture on reaching a certain age, $t_{\rho'}$. In §8.1.1 we suggested two methods of approximating more closely to the true selection ogive, whether such an ogive results from migration to the exploited area, from mesh selection, or from the interaction of both causes.

18.1.1 *The discontinuous approximation*

The method of approximation given in §8.1.1.3 is to sub-divide the ogive describing the changes in F with age into a number of short periods of time during each of which F is taken as constant. (8.7) and (8.8) are the equations for Y_W/R in such circumstances, and we shall use the data of Table 15.7, which define resultant selection ogives for plaice, in order to assess the magnitude of any error that may have arisen previously through over-simplification. The method by which the equations are derived requires the age-axis of the selection ogive to be divided into an appropriate number of equal parts. While this procedure is the simplest for the purpose of exposition, the selection curve will usually be obtained from data in the form of a length ogive, and it is convenient to sub-divide the length-axis of this into equal parts. This will of course mean that the corresponding age axis is not sub-divided quite equally, but is of no consequence if the length and age range over which selection is changing rapidly is not large.

We take the resultant length selection ogive for a 70 mm. cod-end mesh, so that comparison can be made with the simple yield calculation for 'knife-edge' selection with $t_{\rho'} = 3.72$ years. The ogive is given in column D of Table 15.7 and is repeated in column C of Table 18.1, in which are set out the stages for the calculation of (8.7) and (8.8). The first step is to transform this length ogive into an age ogive, and this is done by means of the von Bertalanffy equation for growth in length using the parameter values determined in §16.2.1. The age at each centimetre length from 15 to 32 cm. is tabulated in column B of Table 18.1 and the resulting age ogive is shown as the smooth line in Fig. 18.1, with the original length scale for comparison. Column D gives the intervals of time, Δt, between each age of column B, as fractions of a year. We shall take it that the ogive has reached its asymptote at 32 cm., so that a period of about nine years elapses (i.e. until $t_\lambda = 15$ years) with the fishing mortality at its full value. Column E gives the means of successive pairs of the values in column C; these provide values of the fishing mortality, F_y, as a proportion

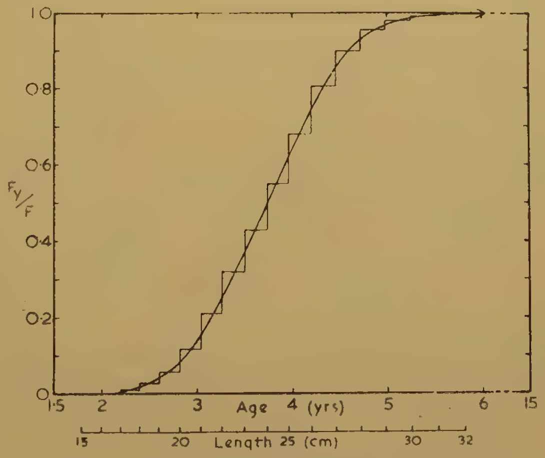


FIG. 18.1
THE DISCONTINUOUS APPROXIMATION TO A SELECTION OGIVE

[Resultant age-selection ogive for plaice with a 70 mm. mesh (from Fig. 15.12) and the approximation to it using the discontinuous method (see Tables 18.1 and 18.2).]

of the asymptotic mortality, F_∞, which proportion we shall assume remains constant over each period Δt. The discontinuous 'steps' thereby produced are shown compared with the age-selection curve in Fig. 18.1. Column E therefore gives the factors by which any value of the asymptotic F_∞ must be multiplied in order to obtain the actual fishing mortality operating during each period Δt, and these latter are shown for $F_\infty = 0.73$ in column F. Intermediate values of F_∞ were used in order to produce the final series of values of Y_W/R, but to show the method it is sufficient to present a single value only.

The next stage is the usual calculation of yield, using the series of F_y corresponding to each value of F_∞ and putting the appropriate value of Δt in place of λ. This gives the yield, $(Y_W)_y$, during the yth period per number present, N_y, at the beginning of the yth period, and these values of $(Y_W)_y/N_y$ are given in column G. Finally, we calculate N_y in terms of the number of fish, R, present at age 1.787 years ($= t_1$ of (8.7)) using a slightly modified form of (8.6). Since there is no pre-exploited phase in plaice when a cod-end mesh of 70 mm. is used, we can put $t_1 = t_\rho$, but in the present case the intervals Δt are not equal; hence (8.6) becomes

$$\frac{N_y}{R} = e^{-\sum_{x=1}^{y-1}(F_x + M)\Delta t_x}$$

and the total yield during the fishable life—this now being between ages 1.787 years and 15 years—is given by the sum of the products of columns G and H, since

$$\frac{Y_W}{R} = \sum \frac{(Y_W)_y}{N_y} \times \frac{N_y}{R}$$

The value of Y_W/R for $F_\infty = 0.73$ calculated in this way is 155.3 gm., those for a full series of F being given in column C of Table 18.2. In order to compare these with Y_W/R for the same mesh calculated by the knife-edge method with $t_{\rho'} = 3.72$ years, we have to adjust the figures of column (R), Fig. 17.1, so that they correspond to the same value of t_ρ as used above, i.e. 1.787 years. This is done by multiplying them by $e^{-M(3.72-1.787)} = 0.8241$, and the resulting values of Y_W/R are given in column B of Table 18.2. It will be seen that values of Y_W/R calculated by the short step method are always less than those calculated from (4.4). The difference is practically negligible at low values of F_∞, but increases as F_∞ increases. The greatest difference is when F_∞ is infinitely high, since all fish are then caught at age 1.787 years according to (8.7) and (8.8) but at 3.72 years according to (4.4). Nevertheless, we may conclude that over the range of F with which we are likely to be concerned in practice, the errors arising through representing entry of plaice to the exploited phase of the population by the knife-edge method of §3.1 can be ignored.

Now this conclusion refers to the pre-war situation when the mesh size in use was such that the age $t_{\rho'}$ was relatively low. At high values of $t_{\rho'}$, with entry to the exploited phase depending solely on selectivity of the gear, we might expect the difference between the two methods to be more pronounced. The reason for this is that the age-selection ogive of a large mesh extends over a relatively greater range of age than does that of a small mesh, owing to the decreasing rate of growth in length with increasing age. The calculation of Y_W/R by the above method is, however, a lengthy process, and to investigate this situation we shall use instead that described in §8.1.1.2, which is to approximate to the ogive by a linear regression. This is not likely to be as accurate as treating the variation of F with age as discontinuous, so we must first test the behaviour of Y_W/R with changes in F predicted by the linear regression method for the mesh size we have already considered.

18.1.2 *The linear approximation*

Fig. 18.2 shows the same ogive as that of Fig. 18.1, (i.e. for plaice with a 70 mm. cod-end mesh) and with a linear regression fitted as defined in §8.1.1.2, giving values

$t' = 2.86$ years

$t'' = 4.65$,,

and having a slope of 0.559, so that

$$k_1 = 0.559F$$

Equation (8.3) can be computed directly, using the above values of t', t'', and k_1, the values of Y_W/R thus obtained being given in column D of Table 18.2. Comparison shows that they lie roughly midway between those of the two previous columns, and so we may conclude that the use of (8.3) with higher values of $t_{\rho'}$ will probably remove about half the error involved in the knife-edge method of representing the function of F with age.

Using the length-selection ogive corresponding to the very high value of $t_{\rho'} = 10$ years, and fitting the linear regression as before, we obtain

$$t' = 8.57 \text{ years}$$

$$t'' = 11.44 \text{ ,,}$$

$$\text{and } k_1 = 0.348\,F$$

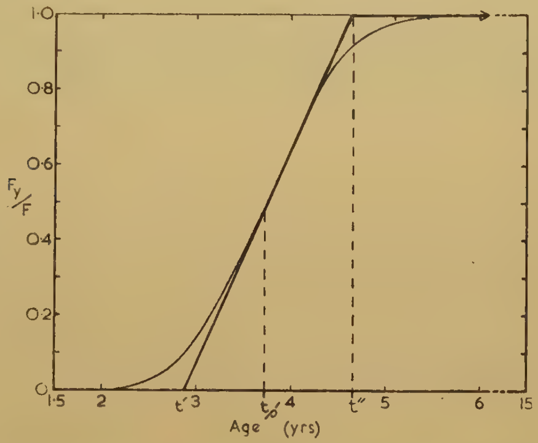


FIG. 18.2
THE LINEAR APPROXIMATION TO A SELECTION OGIVE

[Resultant age selection ogive for plaice with a 70 mm. mesh (as in Fig. 18.1) and the approximation to it using a linear regression of F on t (see Table 18.2).]

Computing (8.3) with these values gives the figures of column F, compared with Y_W/R from (4.4) with $t_\rho = 1.787$ years and $t_{\rho'} = 10$ years (column E). The absolute differences between these columns are a little greater than those between columns B and D, but the percentage differences are similar. Our general conclusion as far as plaice is concerned is therefore that to represent the variation of F with age by the simple knife-edge method of (4.4) is not likely to result in an overestimate of Y_W/R by more than 4%, and this only with the highest values of F_∞ and $t_{\rho'}$ which may be encountered. Consequently, our main conclusions of §17 do not require any modification on this account.

18.2 Density Dependent Natural Mortality

This matter was not discussed in Part III since we have no data available for either plaice or haddock which can give any direct information about this relationship. On the other hand, by making one or two general assumptions, it is possible to make some appreciation of the situation when the natural mortality rate is dependent on population density in the way discussed in §7.3. The fact that, in §17.5.1, we have found the behaviour of population and catch characteristics to be sensitive to changes in natural mortality, makes such an investigation of value despite the lack of data. In this section we consider only plaice, though the same methods would be applicable to other species. It will be remembered that we dealt with the problem of a density dependent mortality rate in two ways in Part II, giving in §7.3.1 a simple approximate method and in §7.3.2 a more rigorous treatment, and we adopt the same procedure here.

In §7.3.1 we proposed a linear relationship (7.8) between the natural mortality coefficient M and the annual mean population number, of the form

$$M = \mu_1 + \mu_2 \bar{P}_N$$

Our first task is to estimate μ_1 and μ_2 for the particular assumptions we shall make concerning the change of natural mortality rate with density; these figures are then used to calculate values of the natural mortality coefficient corresponding to different values of F, and these in turn are used to compute Y_W/R from (4.4). It will be convenient to write (7.8), as

$$M = \mu_1 + (\mu_2 R) \frac{\bar{P}_N}{R} \qquad \text{.. .. .. ..} \qquad (18.1)$$

so that there is no need to obtain values for population number in absolute units.

Hitherto, we have taken the value of $M = 0.1$ in plaice to apply to the pre-war population, and we shall first suppose that in the unexploited population (F = zero) the natural mortality coefficient would be double this value, i.e. 0.2. We cannot obtain direct solutions for M corresponding to each value of F from (18.1), but we can solve iteratively as follows. Taking the values of ${}_1\bar{P}_N/R$ calculated from (5.5) with $M = 0.1$ for $F = 0.73$ and zero, viz. 1.205 and 6.762 respectively, and putting them into (18.1) with M of the left hand side equal to 0.1 and 0.2 respectively, gives the first estimates

$$\mu_1 = 0.0783 \;\; ; \;\; \mu_2 R = 0.0180$$

Using these values, and those of ${}_1\bar{P}_N/R$ for other values of F given in column B of Table 18.3 (i.e. with ${}_1M = 0.1$), we may calculate from (18.1) approximate estimates of the variation of M with F, given in column C. These estimates of ${}_2M$ may now be used in place of the constant value ${}_1M = 0.1$ to calculate second estimates of the population number density, ${}_2\bar{P}_N/R$, given in column D. The values of ${}_2\bar{P}_N/R$ at $F = 0.73$ and zero, viz. 1.205 and 4.476 respectively, provide the second estimates

$$\mu_1 = 0.0631 \;\; ; \;\; \mu_2 R = 0.0306$$

which are then used to calculate third estimates ${}_3M$, and hence ${}_3\bar{P}_N/R$ etc., until no further change takes place. The final series of values of M are shown in column E, and in fact convergence is rapid, these figures differing only slightly from those of column C.

This procedure is rather lengthy, and since we shall need to investigate the effect of other assumptions concerning the variation of M with $\bar{P}_N/R$, the question arises as to whether we can use the special case mentioned in §7.3.1 in which $t_\lambda = \infty$ in the equation for $\bar{P}/_N R$, since then

$$\frac{\bar{P}_N}{R} = \frac{1}{F + M} \qquad \text{.. .. .. ..} \qquad (18.2)$$

and a direct solution for M from (18.1) is possible. Thus putting $F = 0.73$, $M = 0.1$; and F = zero, $M = 0.2$ in (18.2) gives $\bar{P}_N/R = 1.2048$ and 5.000 respectively. By simultaneous equations from (18.1) we have

$$\mu_1 = 0.06825 \;\; ; \;\; \mu_2 R = 0.02635$$

If we substitute for $\bar{P}_N/R$ from (18.2) in (18.1) we obtain a quadratic in M, viz.:

$$M^2 + (F - \mu_1)\, M - (\mu_2 R + \mu_1 F) = 0 \qquad \text{.. ..} \qquad (18.3)$$

which can be solved directly for M for each value of F using the values of μ_1 and $\mu_2 R$ given above (see (7.10)). In this way the figures entered in column F are obtained. It will be seen that they are very similar to those in column E, so that in the present case we may put $t_\lambda = \infty$ and achieve considerable simplification of method without introducing any serious discrepancy.

It remains to be seen how similar the values of M obtained by the simple methods of §17.3.1 are to those which would be obtained by calculating the equivalent constant coefficient $\underline{M}$ from (7.16) of §7.3.2. Using the last values of μ_1 and $\mu_2 R$ above, (7.16) gives the values of $\underline{M}$ entered in column G, which it will be seen are virtually identical to those of the previous column. Our conclusion is, therefore, that for the case we are considering it is not necessary to deal with the exact coefficient $\underline{M}$, but the approximate coefficient defined by (18.1) may safely be used.

We are now in a position to investigate the situations arising when other assumptions are made as to the magnitude of the natural mortality coefficient in the unexploited population. Thus, suppose we take $M = 0.4$ when $F =$ zero. (18.1) and (18.2) then give

$$\mu_1 = -0.1790 \;\; ; \;\; \mu_2 R = 0.2316$$

But a negative value of μ_1 implies that with high values of F, i.e. at low values of $\bar{P}_V/R$, M will itself be negative, which is meaningless. With a linear relationship between M and population number, and with $M = 0.1$ for $F = 0.73$, we evidently cannot have M as high as 0.4 in the virgin stock; the next step is to find the highest possible natural mortality with no fishing that does not imply negative values for either μ_1 or $\mu_2 R$. Putting $\mu_1 = 0$, we have from (18.3),

$$\mu_2 R = M(F + M)$$

and with $M = 0.1$ for $F = 0.73$ this gives

$$\mu_2 R = 0.083$$

With this value of $\mu_2 R$, and putting $F =$ zero in (18.3), we have

$$M = 0.288$$

which is the highest permissible value in the virgin stock. Obviously, such estimates depend partly on the true value of M for the pre-war population, i.e. with $F = 0.73$. In Table 18.4 are therefore given a range of such values with the corresponding maximum permissible values of M when $F =$ zero computed by the above procedure. In this way it is possible to obtain some idea of the range over which the magnitude of M might vary with population density, even though no direct data are available. It must be remembered, however, that the estimates given in Table 18.4 depend on the validity of the assumption that the natural mortality coefficient is linearly related to population number (see §7.3).

It remains to investigate the effect of these changes in M with population density on the shape of the curves of Y_W/R in plaice. The data presented in §14.2.3.3 indicated that M was unlikely to have been greater than 0.1 during the war period when the population density was, on the average, at least three times as high as in the pre-war state. We shall therefore be dealing with a considerable change in M if we take $M = 0.2$ in the unexploited population, since it was found above that the maximum permissible value would be only 0.288 if M is taken as 0.1 for $F = 0.73$. The values of M from column F, Table 18.3, have therefore been used in (4.4) with the corresponding values of F, and the resulting curve of Y_W/R is shown in Fig. 18.3, together with the curve of Y_W/R with a constant $M = 0.1$ for comparison. It will be seen that the effect of M varying in this manner is to reduce the value of $(Y_W/R)_{\max}$ and to increase $(F)_{\max}$ appreciably. A definite maximum in the curve still remains, however, and $(F)_{\max}$ is well below the pre-war value of fishing mortality. Moreover, the change in the curve of Y_W/R is practically negligible above $F = 0.5$, and our conclusions of §17.7 are not changed in any important way.

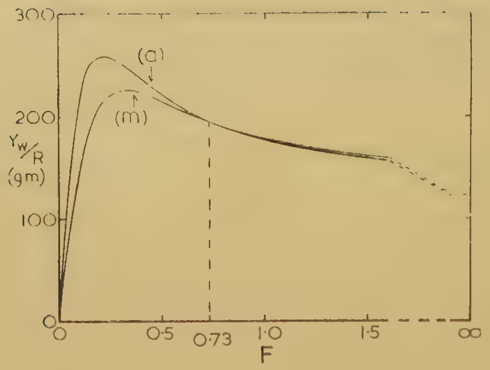


FIG. 18.3 PLAICE: DENSITY DEPENDENT NATURAL MORTALITY

[Yield per recruit, Y_W/R, as a function of F with $t_{\rho'} = 3.72$ yrs. Curve (a) is calculated with constant parameters (see Fig. 17.2); in curve (m) the natural mortality coefficient M varies linearly with population number. See Tables 18.3 and 18.4.]

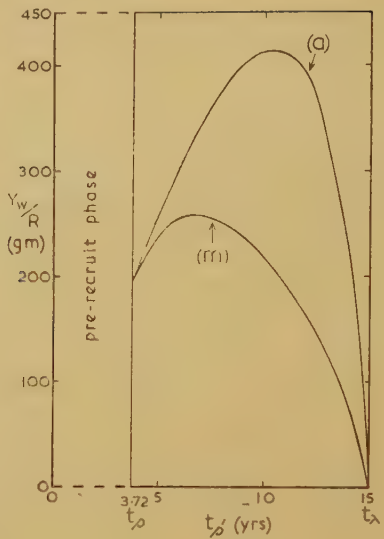


Fig. 18.4 PLAICE: DENSITY DEPENDENT NATURAL MORTALITY

[Yield per recruit, Y_W/R, as a function of $t_{\rho'}$ with $F = 0.73$. Curve (a), constant parameters (see Fig. 17.8); curve (m), natural mortality coefficient M varying linearly with population number as in Fig. 18.3. See Table 18.5.]

Fig. 18.4 shows the corresponding curves for Y_W/R as a function of $t_{\rho'}$, with $F = 0.73$ throughout. The value of M for each value of $t_{\rho'}$ is found by iteration from (18.1) as before, using the same values of μ_1 and $\mu_2 R$ as for Fig. 18.3, and is given in Table 18.5. It will be noted that M reaches its maximum value of 0.2 when $t_{\rho'} = 15$ years, since in these circumstances we are again dealing with the unexploited population. The curve has the same general shape as that with a constant M equal to 0.1, (curve (a)), but the maximum is at a lower value of both $t_{\rho'}$ and Y_W/R. With the natural mortality coefficient dependent on population density in this way, it is still true that a greater annual yield than the pre-war one could apparently have been obtained with a larger mesh-size than was then in use. The estimated potential increase in yield is, however, lower than that with a constant M, as would be expected.

18.3 RECRUITMENT

18.3.1 *Recruitment into several age-groups*

We have shown in §15.1.3 that entry of plaice to the exploited phase of the population was not appreciably influenced by the selectivity of the gear in use before the war but depended mainly on the pattern of the recruitment migration of young fish from the nursery areas and also, though to a lesser extent, on the rejection of undersized fish at sea. A combination of these two factors results in a weight-threshold for entry to the exploited phase. Fish of each year-class are recruited into several age-groups because of size differences between fish of the same age. Hitherto, we have either simplified our models by assuming that all fish of a year-class are recruited at a mean age of $t_{\rho'} = 3.72$ years, or else, in §18.1, treated the recruitment pattern as an age-ogive, analogous to that caused by gear selectivity; in each case it is assumed that all fish of the same age have the same weight. Unlike the situation arising when gear selection alone is operating, however, we have been able to distinguish the recruits of each age sufficiently to show, in §16.3, that their weight-at-age characteristics vary greatly, and have suggested possible ways in which their growth may differ after entering the exploited phase. In this section we use the results of this analysis in investigating the effect on yield curves of recruitment into several age-groups and weight differences between fish of the same age.

We suggested, in §16.3.1, three alternative hypotheses concerning the type of post-recruit growth shown by the recruits into each age-group. These were:—

(i) That the average values of the growth parameters W_∞ and K of each recruit sub-group after entry became the same as the average values in the remainder of the exploited population, so that the weights-at-age of post-recruits differ only by reason of their differing pre-recruit growth (hypothesis (j)).

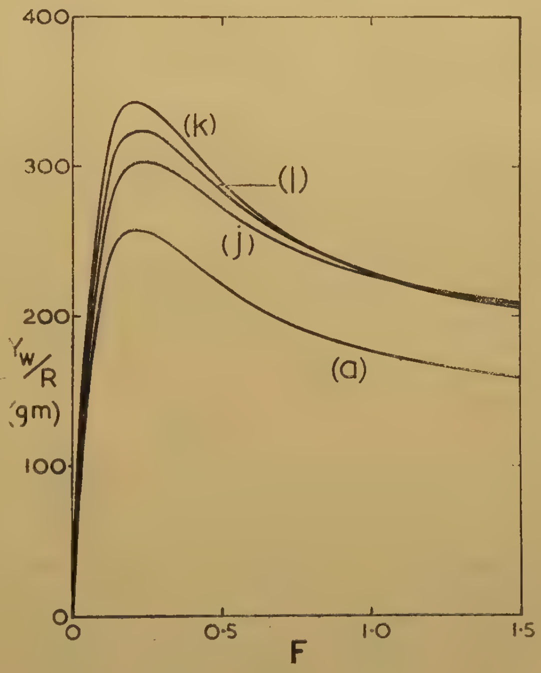
(ii) That the various pre-recruit growth rates of each recruit sub-group are related to, and can be described by, differing values of the growth parameter W_∞, which persist in later life (hypothesis (k)).

(iii) That the differing pre-recruit growth rates of each recruit sub-group are related to, and can be described by, values of K which persist in later life (hypothesis (l)).

Here we need to compute the curve of Y_W/R with respect to F for each of these hypotheses. This may be done by means of (9.13), calculating the yield from each recruit sub-group using the appropriate values of t_ρ from Table 15.7 and the growth parameters corresponding to each of the above hypotheses given in Table 16.8. Each such yield is then weighted by the proportion that the recruit sub-group is of the total annual recruitment (row E, Table 15.8), the results being tabulated in columns A-D of Table 18.6. These are finally summed to produce the required total values of Y_W/R given in columns E and plotted in Fig. 18.5. The curve of Y_W/R computed from (4.4) in the usual way is shown for comparison as (a).

FIG. 18.5 PLAICE:
EFFECT OF WEIGHT DISPERSION AND RECRUITMENT INTO SEVERAL AGE-GROUPS

[Curve (a) is the ordinary yield curve calculated from (4.4); it implies that all fish of a given age are the same weight and that each year-class is recruited at $t_\rho' = 3.72$ yrs. Curves (j), (k) and (l) are calculated from hypotheses of these designations developed in §16.3 concerning possible forms of weight dispersion within each year-class, together with the pattern of recruitment into several age-groups implied by them. See also Table 18.6.]



It will be seen that all three hypotheses result in yield curves that lie above curve (a) over their whole range, but there are two factors that must be borne in mind when comparing these curves. One is that all three hypotheses predict rather higher mean weights for fully recruited age-groups than were found from data, as can be seen from Table 16.9 by comparing columns B, C and D with column E; these amount to roughly 4% for hypothesis (j), 7% for (l) and 10% for (k). The other is that the weight-at-age data used in §16.3.1 for estimating the average weight of fish in each recruit sub-group could not be adjusted for fish below 23 cm. rejected at sea in the way that the age-composition data had been; as a result, the average weight of each recruit sub-group predicted by all three hypotheses is about 150 gm. (see Table 16.8), whereas that corresponding to the mean age at recruitment of 3.72 years (used in computing curve (a)) is 123 gm. Both these factors tend to make curves (j), (k) and (l) too high when comparing them with (a), and although their precise effect cannot be assessed it is responsible for at least the greater part of the differences shown in Fig. 18.5.

Although it seems from this that the yield per recruit may be slightly underestimated by ignoring weight dispersion among fish of the same age and using a mean age at recruitment, what matters from the point of view of assessing errors in predictions is whether this simplification causes any distortion in the shape of the yield curve. This can be seen best by adjusting each curve to the same value at the pre-war fishing mortality of $F = 0.73$ (cf. 17.5), and the results are given in column F of Table 18.6. The figures are now so similar that they cannot usefully be shown graphically, and are therefore summarised as follows:

F	*Hyp.* (j)	*Hyp.* (k)	*Hyp.* (l)	*Curve* (a) *of Fig.* 18.5
0.01	32.9	38.7	35.1	36.9
0.05	128.9	149.5	137.2	143.8
0.1	194.6	220.0	205.8	214.8
0.2	237.5	262.9	248.4	257.2
0.3	237.1	255.4	245.6	251.9
0.4	226.6	238.5	232.2	236.2
0.5	214.8	221.7	218.1	221.0
0.73	194.4	194.4	194.4	194.4
1.0	179.5	175.6	177.1	176.6
1.5	165.1	157.5	160.3	159.1

It will be seen from inspection that such differences as remain are confined to low values of F in the region of $(Y_W/R)_{\max}$. As before, the figures for hypothesis (k) are the highest, but now those of curve (a) are within one or two per cent. of them and are above those for the remaining hypothesis. In §16.3.2 we concluded that the weight dispersion pattern predicted by hypothesis (k) agreed most nearly with that found in samples of fully recruited age-groups but that this hypothesis tended to exaggerate the degree of dispersion. The fact that the figures for curve (a) are slightly below the adjusted figures for hypothesis (k) therefore indicates that it is a permissible simplification to ignore differences in weight of plaice of the same age and to use mean values of W_∞ and K in conjunction with a mean age at recruitment.

18.3.2 *Density dependent recruitment—self-regenerating population models*

From the investigation in §§6.1.1 and 6.1.2 of possible relationships between egg-production and recruitment, we concluded that the simplest acceptable one was that defined by (6.10), namely

$$R = \frac{1}{\alpha + \beta/E}$$

In §6.1.4 this relationship was introduced into expression (4.4) for yield to give the self-regenerating population model (6.23), which can be written in the form

$$Y_W = \frac{Y_W/R}{\alpha}\left(1 - \frac{\beta}{\gamma}\right)$$

where the quantity γ denotes the annual egg-production per recruit, and is given in full by (6.21), viz.:

$$\gamma = \frac{E}{R} = W_\infty \left[e^{-M(t_\eta - t_\rho)} \sum_{r=0}^{H} s_r p_r \chi_r e^{-Mr} (1 - e^{-K(t_\eta + r - t_0)})^3 + \right.$$

$$\left. + e^{-M_\rho - (F+M)(1-h)} \sum_{r=H+1}^{H+\mathcal{J}+1} s_r p_r \chi_r e^{-(F+M)(r-H-1)} (1 - e^{-K(t_\eta + r - t_0)})^3 \right] \quad .. \quad (18.4)$$

It will be remembered (see §15.2.3.1) that there were insufficient data to analyse the relationship between population size and subsequent recruit number in plaice. The information for haddock on the other hand, while not sufficient to allow a precise determination of α and β to be made, nevertheless gave some idea of the range of values that these parameters might have. Several such pairs of values were given on p. 273, the $E - R$ curve produced by each being shown in Fig. 15.15. Here we use them to examine the effects that are to be expected as a result of the dependence of recruitment on egg-production.

No attempt is made at this stage to vary any parameters other than recruitment, so that computing γ from (18.4) is a straightforward, though lengthy, task; some comment is needed, however, on the values used for the parameters that are specific to this equation. The age at first maturity, t_η, of the haddock is 2 years. Values of the sex-ratio s, the percentage maturity p and the fecundity ξ from this age upwards are given in Table 15.10. The parameters M, K, W_∞, t_0 and t_ρ were estimated in the appropriate sections of Part III and are tabulated in Fig. 17.24, while the age $t_{\rho'}$ corresponding to the 70 mm. cod-end mesh size in use in the haddock fishery before the war is 1.83 years. Hence the remaining parameters in (18.4) are, for this mesh,

$$H = 0$$

$$h = 0.83$$

$$\mathcal{J} = 8$$

Values of Y_W/R for each value of F are calculated in the usual way from (4.4) and are the same as those given in the legend to Fig. 17.24. The resulting curves of absolute yield, Y_W, as a function of F, for each pair of values of α and β, are shown in Fig. 18.6, together, for comparison, with the curve computed from (4.4) with recruitment constant (curve (a)). They are lettered according to the key given on p. 273 and Fig. 15.15; it will be remembered that the values of β, and the tendency to a proportional relationship between E and R within the range of egg-production involved, increase from curves (p) to (t).

The most obvious feature of the curves of Fig. 18.6 is the very high yield at low values of F that results when high values of β are used. At the same time the change in the position of $(F)_{\max}$ is slight, and is in a direction that *decreases* its value from that in curve (a). At values of F greater than 1.0 (corresponding to the pre-war state) all curves in which recruitment varies with density descend more rapidly than if recruitment is constant, and eventually the yield becomes zero. This behaviour has not been met in any of our previous population models, and it results from there being insufficient spawners to produce the number of eggs necessary to maintain the population in a steady state; in other words, it

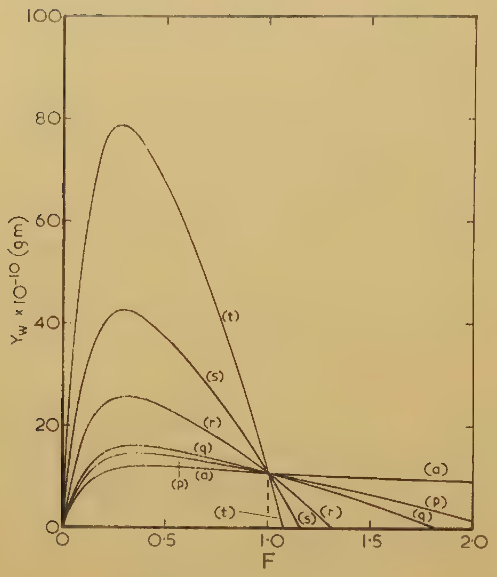


FIG. 18.6 HADDOCK:
DENSITY DEPENDENT RECRUITMENT

[Absolute yield, Y_W, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.24); curves (p) to (t) recruitment varying with egg-production according to the curves of Fig. 15.15 and values of α and β given on p. 273. The very high maxima resulting from a pronounced change of recruitment with egg-production (e.g. curve (t) should be contrasted with the maxima of Fig. 18.17 where growth as well as recruitment is made to vary with density.]

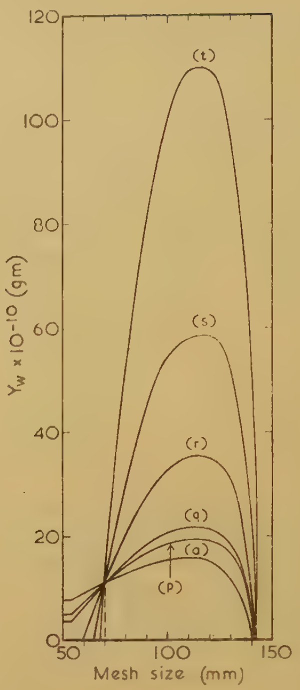


FIG. 18.7 HADDOCK:
DENSITY DEPENDENT RECRUITMENT

[Absolute yield, Y_W as a function of mesh with $F = 1.0$. Curve (a) constant parameters; curves (p) to (t) recruitment varying with egg-production as in Fig. 18.6. Contrast with Fig. 18.18 for effect of density dependent growth.]

implies that the population would eventually become extinct if a sufficiently large value of F were to be maintained for a long enough period.

The curves of Fig. 18.7 show the variation of Y_W with mesh size, with $F = 1.0$, for the same pairs of values of α and β. These are computed from (18.4) as before, except that the parameters H, h and J are, of course, different for each mesh. As in Fig. 18.6, there is a striking increase of $(Y_W)_{\max}$ as the value of β is increased, but only a slight lateral shift in its position. It will also be noted that at certain small mesh sizes, according to the particular value of β, the population becomes extinct; this is again due to inadequate egg-production, resulting in this case from the use of a very small mesh in conjunction with a rather high fishing mortality rate.

It seems therefore that, compared with predictions from a simple model with constant recruitment, any relationship between recruitment and population density of the same general pattern as we have used would tend to enhance the possible increases in yield that might be obtained either with a lower fishing intensity or a larger cod-end mesh than those used before the war. At the same time, it is clear that a self-regenerating model in which all parameters other than recruitment are held constant can predict such extreme changes in density that compensating changes in growth and possibly natural mortality would be certain to occur in practice. Thus it is not even possible to draw the yield curves for the highest value of β shown in Fig. 15.15 on the scale used in Figs. 18.6 and 18.7, since $(Y_W)_{\max}$ in these is about a hundred times greater than the pre-war mean yield. A further study of the properties of self-regenerating models will therefore be postponed until §18.5.2, where both recruitment and growth are made to vary simultaneously with density.

18.4 DENSITY DEPENDENT GROWTH

It will be remembered that the problem was discussed in §9.4 in two stages. We first dealt with it more or less empirically (§9.4.2) for the case in which there were available data referring to growth at various levels of population density over a suitable range. Then, in §9.4.3, we undertook a further analysis in terms of the amount of food consumed annually by a population and the corresponding growth rate, finally introducing the concept of the grazing power of a fish population and the interaction between the latter and the organisms on which it was feeding.

Data presented in §16.4.1.2 seemed to indicate that for the haddock a linear relationship between the growth parameter L_∞ and population numbers might be satisfactory. For the plaice, on the other hand (§16.4.1.1), the data gave only two estimates of growth rate and the corresponding population biomass, so that we had no option but to relate them linearly. In this species, therefore, it is particularly necessary to attempt a further analysis of the problem, and this will be undertaken in §18.4.2, one object being to see whether the use of a linear relationship is likely, in fact, to give satisfactory results.

18.4.1 *Empirical relationships between growth and population density—hypothesis* (*b*)

The data on which our analysis is based, and the relevant discussion, have been given in §16.4.1. The problems we are concerned with here are only those of computation, following the general principles set out in §9.4.2. The reader is reminded that we were led to propose a linear relationship between the growth parameter L_∞ and biomass, $\bar{P}_W$, in plaice, and between L_∞ and population numbers, $\bar{P}_N$, in haddock. In order to calculate the equation for Y_W/R incorporating these relationships we have to obtain values of W_∞ corresponding to each fishing mortality or cod-end mesh size (see below). This amounts, in plaice, to solving simultaneously a set of equations which have already been presented in Part II but which, for convenience, are restated as follows:—

$$L_\infty = a + bR\left(\frac{\bar{P}_W}{R}\right) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (18.5)$$

$$\frac{\bar{P}_W}{R} = W_\infty \sum_{n=0}^{3} \Omega_n e^{-nK(t_\rho - t_0)} \left\{ \frac{1 - e^{-(M+nK)\rho}}{M + nK} + \frac{e^{-(M+nK)\rho}\left(1 - e^{-(F+M+nK)\lambda}\right)}{F + M + nK} \right\} \quad \ldots \quad \ldots \quad (18.6)$$

$$t_0 = t_{\rho'} + \frac{1}{K} \log\left(\frac{L_\infty - L_{\rho'}}{L_\infty}\right) \quad \ldots \quad \ldots \quad \ldots \quad (18.7)$$

$$t_{\rho'} = t_\rho + \frac{1}{K} \log\left(\frac{L_\infty - L_\rho}{L_\infty - L_{\rho'}}\right) \quad \ldots \quad \ldots \quad \ldots \quad (18.8)$$

$$W_\infty = qL_\infty^3 \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (18.9)$$

For haddock, in addition to (18.7), (18.8) and (18.9), we require

$$L_\infty = a + bR\left(\frac{\bar{P}_N}{R}\right) \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad \ldots \quad (18.10)$$

$$\frac{\bar{P}_N}{R} = \frac{1 - e^{-M\rho}}{M} + \frac{e^{-M\rho}\left(1 - e^{-(F+M)\lambda}\right)}{F + M} \quad \ldots \quad (18.11)$$

It will be realized that in cases where growth depends on population density we should not wish to investigate the behaviour of Y_W/R as a function of the *age* at which fish enter the exploited phase, since a given value of $t_{\rho'}$ is no longer associated with fish of the same size nor therefore with a particular size of mesh. As we shall be concerned only with changes in the growth rate of fish after they have entered the exploited area, their length on entering it, L_p, and the corresponding age, t_p, remain constant throughout; but subsequent entry to the exploited phase can be defined only in terms of the length, $L_{p'}$, corresponding to the mean of the selection ogive of the gear in use. It is for this reason that we have to include (18.8) above for $t_{p'}$ in terms of $L_{p'}$, and to illustrate yield curves as functions of cod-end mesh size instead of the mean selection age $t_{p'}$. Some simplification of this scheme is possible in the calculation of yield with respect to F in plaice with the pre-war mesh of 70 mm., since in this case $t_p = t_{p'}$, and Y_W/R can therefore be obtained directly from $\bar{P}_W/R$ by means of the equation

$$\frac{Y_W}{R} = F\frac{\bar{P}_W}{R} \quad \ldots \quad (18.12)$$

Two general methods of solving these equations have been used for given values of F or mesh size:

(a) A graphical method has been used to calculate Y_W/R as a function of F in plaice with a 70 mm. mesh. For each value of F we take a range of values of W_∞, which we call ${}_1W_\infty$, and calculate corresponding values of ${}_2W_\infty$ from the equation

$${}_2W_\infty = q\left\{a + bR\ {}_1W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{p'} - {}_1t_0)}}{F + M + nK}\left(1 - e^{-(F+M+nK)\lambda}\right)\right\}^3$$

formed by combining (18.5), (18.6) and (18.9) above, with ${}_1t_0$ being given in terms of ${}_1W_\infty$ by (18.7), using the values of q, a and bR appropriate to plaice given in §16.4.1.1, viz.:

$$q = 0.00892$$

$$a = 72.47 \text{ cm.}$$

$$\text{and } bR = -0.0149$$

We require a value of ${}_1W_\infty$ for each value of F such that ${}_1W_\infty = {}_2W_\infty$ in the above equation. This can be obtained by plotting a number of values of ${}_1W_\infty$ against the corresponding values of ${}_2W_\infty$, and the point on this graph where ${}_1W_\infty = {}_2W_\infty$ is the required value of W_∞. This procedure is shown in Fig. 18.8, from which was obtained the series of W_∞ given in column B of Table 18.7.

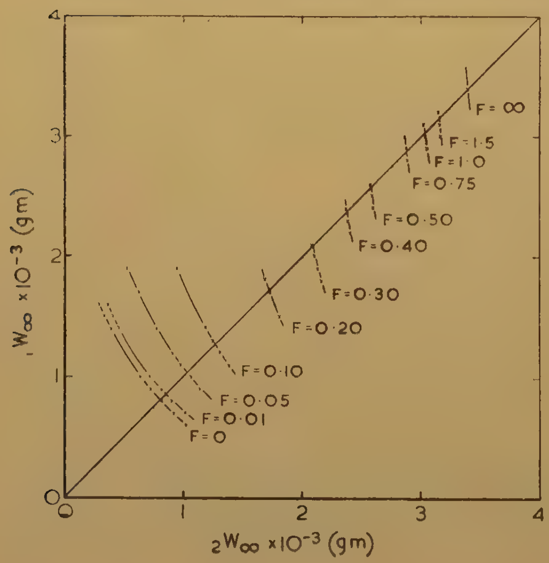


FIG. 18.8 PLAICE:
DENSITY DEPENDENT GROWTH

[Graphical method of solving for W_∞ at given values of F with L_∞ linearly related to biomass. See also text and Table 18.7.]

(*b*) Curves of yield as a function of cod-mesh size in plaice and as functions of fishing mortality and cod-end mesh size in haddock have been obtained by an iterative method. For example, the calculation of W_∞ as a function of F in haddock by iteration proceeds as follows. Putting into (18.10) the values of ${}_1\bar{P}_N/R$ for each value of F, with $t_{\rho'} = 1.83$ years, we calculate ${}_2L_\infty$ for each value of F using the estimates of a and bR for haddock given in §16.4.1.2, namely

$$a = 56.88 \text{ cm.}$$

$$bR = -2.636$$

The constant value of L_ρ in haddock is found from the growth parameters of §16.2.2 to be 17.95 cm.; we can therefore calculate the series of ${}_2t_{\rho'}$ corresponding to each value of ${}_2L_\infty$ from (18.8) above, and hence the second estimates ${}_2\bar{P}_N/R$ from (18.11). These give values of ${}_3L_\infty$ from (18.10) and the cycle of operations is repeated until consecutive estimates of L_∞ are not appreciably different. Finally, we calculate the series of W_∞ from these values of L_∞ by means of (18.9). The results are given in Table 18.7 (column C) together with the final series of $t_{\rho'}$ in column D. This method has the great advantage that it is practically impossible for computational errors to influence the final estimate. It is necessary, however, for successive estimates of the various parameters to converge reasonably quickly, and this does not happen with some of the calculations of §18.4.2, where the graphical method had to be used. In the calculations of this section it was found that the third and fourth estimates were virtually identical.

Whichever method of calculation is adopted, the final step is to calculate values of Y_W/R for each value of F. In plaice, with a 70 mm. mesh, these can be obtained at once from (18.12) but in haddock we need first to compute revised values of t_0 from (18.7) which can then be inserted in (4.4) together with the final estimates of W_∞ and $t_{\rho'}$ from Table 18.7. In this way changes in growth are restricted to the post-recruit phase of the population as is desired. It is important to note that the value of $t_{\rho'}$ in haddock changes with F, even although the mesh size is the same throughout. This is because the time taken for fish to grow from the length L_ρ at which they are recruited, to the constant mean selection length $L_{\rho'}$, is influenced by the density of the exploited phase.

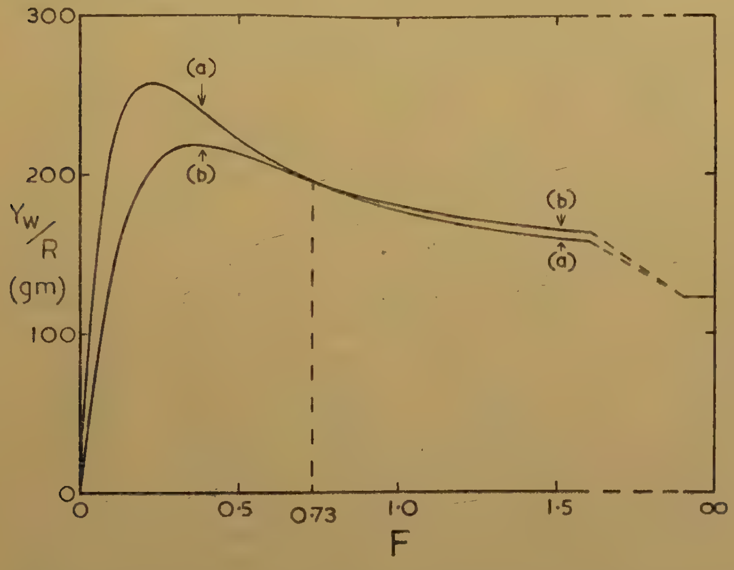


FIG. 18.9 PLAICE: DENSITY DEPENDENT GROWTH

[Yield per recruit, Y_W/R, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.2); curve (b) growth density dependent, using a linear relation between L_∞ and biomass, $\bar{P}_W/R$. See Table 18.7.]

The parameters of Table 18.7 are used to construct curves of yield with respect to fishing mortality for the plaice and haddock. These are shown as curves (b) in Figs. 18.9

and 18.10 respectively, together with the curves of Figs. 17.2 and 17.24 in which growth remains constant throughout for comparison (curves (a)). In both species the effect of introducing the dependence of growth on population density is seen to be that $(F)_{\max}$ is increased and $(Y_W/R)_{\max}$ decreased, though these changes are relatively less in haddock than in plaice. With fishing mortalities higher than 0.73 in plaice and 1.0 in haddock, the values of Y_W/R are greater than with a constant growth rate, though the increase for both species is small within the range of F we have considered.

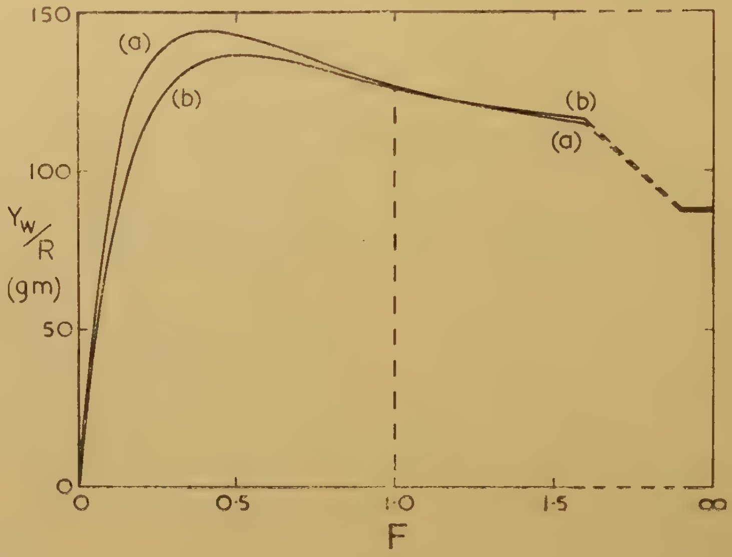


FIG. 18.10
HADDOCK:
DENSITY DEPENDENT GROWTH

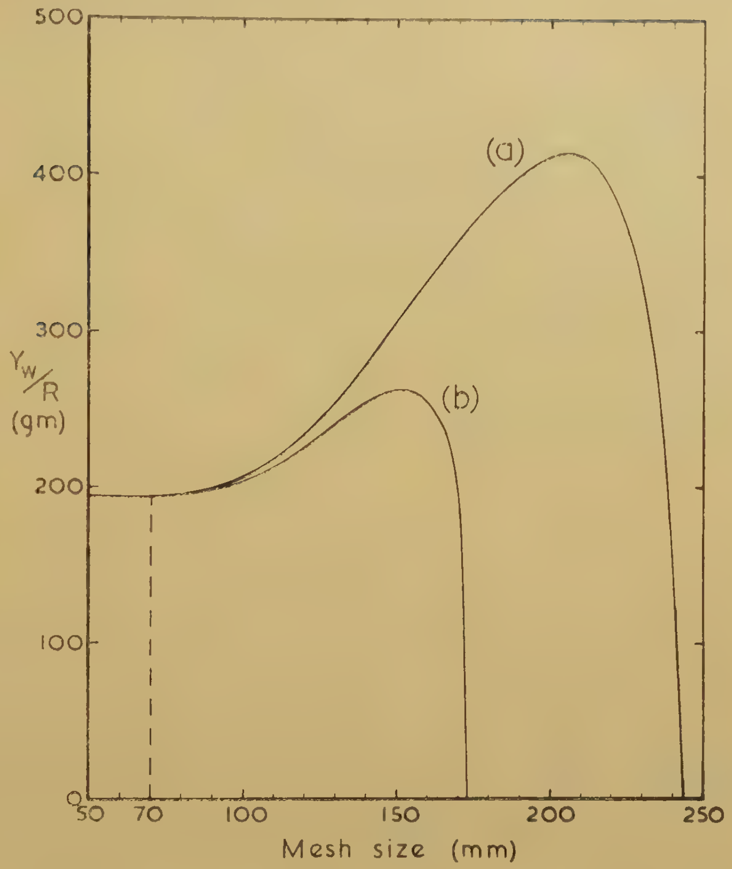
[Yield per recruit, Y_W/R, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.24); curve (b) growth density dependent, using a linear relation between L_∞ and population numbers, $\bar{P}_N/R$. See Table 18.7.]

The calculation of Y_W/R as a function of mesh size makes use of the same set of equations except that in plaice (18.8) is required in addition to those used previously. As usual, we take F constant at 0.73 in plaice and 1.0 in haddock. The series of cod-end mesh sizes used are given in columns A and D of Table 18.8. The reason they are not whole numbers is that all but the last in each column correspond to certain integral values of $t_{\rho'}$ when $W_\infty = 2867$ gm. in plaice and 1209 gm. in haddock, thus allowing previously calculated values of $\bar{P}_W/R$ and $\bar{P}_N/R$ to be used to begin the process of iteration. The final estimates of W_∞ and $t_{\rho'}$ for each species are given in columns B, C and E, F, respectively.

It will be noticed that the limiting sizes of cod-end mesh are those which correspond to $W_\infty = 808$ gm. in plaice and 880 gm. in haddock. The growth defined by these values is such that fish reach the mean selection size (at which they are retained by those meshes) only at age $t_{\rho'} = 15$ years in plaice and $t_{\rho'} = 10$ years in haddock. These are, of course, the values of t_λ that we have used. In other words, a cod-end mesh size of about 170 mm. or above in plaice would, according to the theoretical model, result in such a high population density, and consequently slow rate of growth, that all fish die at age t_λ before they have become large enough to be retained by such meshes; hence the value of Y_W/R is zero. This phenomenon is encountered on several occasions in later sections, and in view of the abundant evidence, summarised in §9.4.1, that the growth rate of adult fish can vary within wide limits without ill-effect, we shall regard it as reasonable to expect growth to decrease to this extent in practice without causing an appreciable increase in natural mortality. We should not expect, however, that the yield would *suddenly* become zero at a certain mesh size; that is the result of postulating that all surviving fish die when age t_λ is reached, that all individuals at any age are the same weight and that mesh selection is 'knife-edge'. This procedure minimises the danger of overestimating the benefits of making extremely large changes in mesh size, but if a more exact prediction was required in a particular case the possible errors thus involved could be examined by putting t_λ to infinity, as in 17.5.2.

FIG. 18.11
PLAICE:
DENSITY DEPENDENT
GROWTH

[Yield per recruit, Y_W/R, as a function of mesh size with $F=0.73$. Curve (a) constant parameters (Fig. 17.8 plotted on mesh scale); curve (b) growth density dependent, using a linear relation between L_∞ and $\bar{P}_W/R$ as in Fig. 18.9. The effect of introducing a density dependent growth is more marked on yield-mesh curves than on yield-fishing mortality curves. See also Table 18.8.]



Figs. 18.11 and 18.12 show curves of yield with respect to cod-end mesh size in plaice and haddock respectively. They were calculated from (4.4) using the values of W_∞ and t_ρ given in Table 18.8. The curves of Figs. 17.8 and 17.25 with growth constant are shown for comparison, the $t_{\rho'}$ scale being transformed to mesh size using the appropriate constant values of W_∞ (i.e. 2867 gm. in plaice and 1209 gm. in haddock). Noticeable changes when the variation of growth with density is introduced are that the size of mesh giving the greatest value of Y_W/R is very much reduced, particularly in plaice, and the values of $(Y_W/R)_{\max}$ are themselves considerably lower.

We must therefore conclude that the dependence of growth on population density is of considerable importance, since failure to take it into account would probably result in overestimating the potential increases in yield that could be obtained by reducing fishing intensity or, particularly, by increasing mesh-size from the pre-war values. However, $(F)_{\max}$ in Figs. 18.9 and 18.10 is still well below the pre-war fishing mortality in both species, and the cod-end mesh sizes giving the maximum yield are also above those that were in use before the war. Consequently, the conclusions of §17.7 still stand.

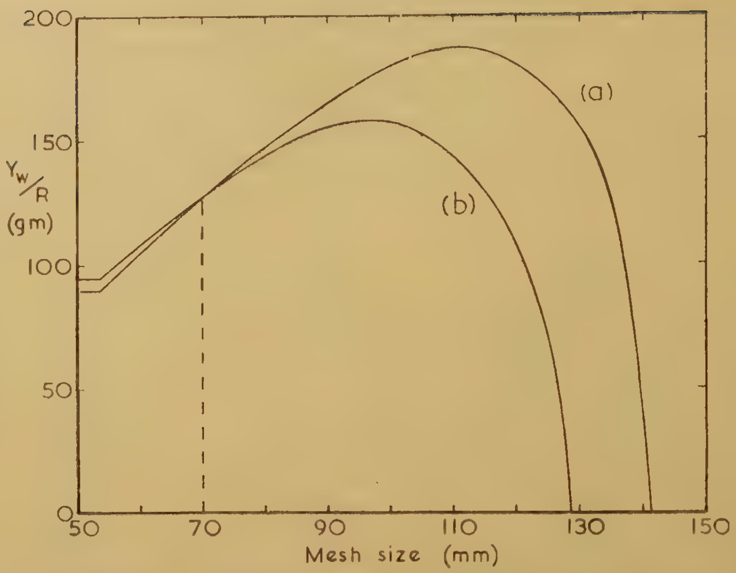
18.4.2 *Dependence of growth on food supply*

18.4.2.1 *Estimation of the annual food consumption,* Ξ

In §9.4.3.2 several hypotheses were developed concerning the possible relationship between the availability of food and the amount consumed, leading to equations giving the annual food consumption of the population, Ξ, in terms of the main variables with which we are concerned here, viz. the fishing mortality F and the corresponding growth parameter W_∞. The principal observed state of the plaice population for which we have estimates of F and W_∞ is that during the ten years immediately preceding the war, when the

FIG. 18.12
HADDOCK:
DENSITY DEPENDENT
GROWTH

[Yield per recruit, Y_W/R, as a function of mesh size with $F = 1.0$. Curve (a) constant parameters (Fig. 17.25 converted to a mesh scale); curve (b) growth density dependent, using a linear relation between L_∞ and $\bar{P}_N/R$ as in Fig. 18.10. As in plaice, the effect on yield-mesh curves of the density dependence of growth is more marked than on yield-fishing mortality curves (cf. Fig. 18.10). See also Table 18.8.]



mean value of F was 0.73 and that of W_∞ was 2867 gm. The first quantity to find is therefore the mean annual food consumption of this population, since the equations corresponding to each hypothesis must imply this rate of consumption of food when F and W_∞ have the above values.

Our analysis of Dawes' data on the maintenance and growth requirements of the plaice (§16.4.2) gave definite evidence of a variation in efficiency of utilisation of food with the amount consumed, and provided estimates of the coefficients of Kostitzin's equation (9.26), which takes this effect into account. In the following analysis we shall therefore use (9.32) to compute the annual food consumption by the population per recruit, writing it as

$$\frac{\Xi}{R} = \frac{1}{\varepsilon_0}\left\{(Q + 3KW_{\infty M}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W\right\}\tanh^{-1}\left\{\frac{(Q + 3KW_\infty^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}{(Q + 3KW_{\infty M}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}\right\} \quad \ldots \quad \ldots \quad (18.13)$$

With $F = 0.73$ and $W_\infty = 2867$ gm., and with the values determined in §16.4.2.3., viz.:

$$\varepsilon_0 = 0.51$$

$$Q = 10.05$$

$$W_{\infty M}^{1/3} = 67.6$$

this expression gives

$$\frac{\Xi}{R} = 1122 \text{ M-g-es.}$$

which we shall take as our estimate of the annual mean food consumption per recruit of the pre-war plaice population. It will be noted that this value is in terms of the type of food used in Dawes' experiments, and is consequently in the units 'Mytilus-gram-equivalents'; in the following we abbreviate the latter to 'M-g-es'.

18.4.2.2 *Hypotheses* (*a*) *and* (*c*)

Hypothesis (*a*), the simplest we have used concerning the relation between availability of food and food consumption of the population, is that the total amount of food available is unlimited, so that growth is independent of population density. This is, in effect, the situation implied throughout §17 where we put $W_\infty = 2867$ gm. for all values of F. It is therefore of interest to see what food consumptions would be predicted from (18.13) for values of F other than 0.73, with the growth rate constant at its pre-war value. These are the series of Ξ/R given in column B of Table 18.9, and it will be seen that they change over a 20-fold range between $F = 0$ and $F = 1.5$—a very considerable variation. It is perhaps rather unlikely that the productivity of the food organisms is great enough to supply such differing amounts of food for consumption by the fish population without its availability to the latter being affected. We therefore turn to *hypothesis* (*c*), which may be regarded as the opposite of hypothesis (a). It is that a certain constant amount of food is available for consumption each year, and that this amount is always consumed by the fish population whatever the density of the latter may be. If we take the pre-war value of 1122 M-g-es. as an estimate of the food available per year, then from (18.13) we can calculate the resulting value of W_∞ for each value of F. We use graphical methods for this calculation, as with most of those in §8.4.2, since the series of W_∞ obtained by iteration converges very slowly. In this instance we calculate Ξ/R with a given value of F, for each of a set of values of W_∞; then, by plotting Ξ/R against W_∞ and reading off from the curve at $\Xi/R = 1122$, we obtain the required value of W_∞ for this fishing mortality.

The series of W_∞ given in column D of Table 18.9 was obtained in this way, and we find that for values of F equal to or less than 0.34, the corresponding values of W_∞ are less than $W_{\rho'}$, i.e. 122.9 gm. In other words, when $F = 0.34$ the population is of a size such that the available food is only just sufficient to supply maintenance requirements; thus the fish remain throughout life at the weight at which they entered the exploited area. This is, of course, similar to the phenomena encountered at very high mesh sizes in the preceding section except that it is more extreme, since we now have not just a very slow rate of growth but no growth at all. However, the few data which exist relating to North Sea plaice when the population density has been high, such as during the 1914-18 and 1939-45 wars and the earliest stages of exploitation, do not suggest that growth ceases even when the population density is as high as that in the virgin stock. Moreover, since hypothesis(c) implies negative growth at values of $F < 0.34$, i.e. that fish would 'shrink' after entering the exploited area, we must consequently reject it as predicting too great a change in growth.

18.4.2.3 *Hypotheses* (*d*) *and* (*e*)

Hypotheses (*d*) *and* (*e*) of §9.4.3.2.2 introduce a concept discussed by Ivlev (1945) not included in the simple hypotheses above. In general terms, this is that the amount of food consumed by a fish per unit time is partly dependent on its *intensity of feeding;* this, in turn, depends on the extent to which its actual food consumption falls short of the maximum amount of food it would consume per unit time if food were available to it in unlimited supply.

To interpret Ivlev's concept in the case of a fish population living under natural conditions we have to decide how to define the *available food.* Thus, in *hypothesis* (*d*) we have taken the total food available per year to the population as constant, and assumed that the proportion available to each fish is that total amount divided by the population numbers. In §9.4.3.2.2 it was shown that this leads to (9.35), which, in terms of the annual food consumption per recruit, becomes

$$\frac{\Xi}{R} = \frac{\Xi_L}{R}\left(1 - e^{-h_1 R/\Xi_L}\right) \qquad .. \qquad .. \qquad .. \qquad (18.14)$$

Now Ξ_L/R, which is the maximum amount of food that can be eaten during a year by a given population (per recruit), can be determined for the pre-war plaice population from the modified form of (9.34), viz.:

$$\frac{\Xi_L}{R} = \frac{1}{\varepsilon_0}\left\{(Q + 3KW_{\infty M}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W\right\}\tanh^{-1}\left\{\frac{(Q + 3KW_{\infty L}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}{(Q + 3KW_{\infty M}^{1/3})\bar{P}_{W^{2/3}} - 3K\bar{P}_W}\right\} \qquad .. \qquad .. \qquad (18.15)$$

Using the value of $W_{\infty L}$ determined in §16.4.2.3, viz. 16000 gm., and putting $F = 0.73$, this gives

$$\frac{\Xi_L}{R} = 1471 \text{ M-g-es.}$$

We can now determine the value of the constant h_1 of (18.14) by inserting this value of Ξ_L/R and that of Ξ/R already obtained, viz.: 1122 M-g-es. This gives:

$$h_1 = 2116$$

To investigate the changes in growth rate with various population densities that would be predicted from hypothesis (d) we have to find, for any value of F, a value of W_∞ that will satisfy both (18.13) and (18.14). This may be done graphically, as follows. For each value of F we calculate Ξ/R and Ξ_L/R from (18.13) and (18.15) using a series of values of W_∞. But for each value of Ξ_L/R we have another estimate of Ξ/R from (18.14). Plotting both series of estimates of Ξ/R against W_∞, we get two curves whose intersection gives the required W_∞. Values of W_∞ obtained in this way are given in column E of Table 18.9. As with hypothesis (c), values of W_∞ less than $W_\rho = 122.9$ gm. are obtained with low values of F, though in this case the limiting value of F is a little smaller (about 0.24). Another difference is that W_∞ for values of F greater than 0.73 does not become as great as with hypothesis (c). In fact, it reaches the limit $W_{\infty L} = 16000$ gm. as $F \rightarrow \infty$, whereas before, W_∞ became infinitely great in these circumstances.

We have therefore achieved some improvement by introducing the concept of 'intensity of feeding' and by setting a limit to the amount consumed by a population when food is in unlimited supply, but hypothesis (d) still fails to account satisfactorily for the growth characteristics under conditions of high population density. It may be suspected that this is partly due to the interpretation given to 'available food', since an implication of hypothesis (d) is that the total food is, in effect, divided into portions, each fish having access to one portion only. In *hypothesis (e)*, on the other hand, we assume that the total food available per year to the population is proportional to the number of fish in it; the food available to an individual fish therefore becomes independent of population density and its food consumption is limited only by its 'appetite'. It was shown in §9.4.3.2.2 that hypothesis (e) leads to the equation

$$\frac{\Xi}{R} = \frac{\Xi_L}{R}\left(1 - e^{-h_2(P_N/R)\,(R/\Xi_L)}\right) \quad .. \quad .. \quad .. \quad (18.16)$$

and inserting the values of Ξ/R and Ξ_L/R for the pre-war population determined above, we find

$$h_2 = 1757$$

The values of W_∞ for each value of F that are predicted by hypothesis (e) may be obtained by the same graphical method as before, except that the required values of W_∞ are now those that satisfy simultaneously (18.13), (18.15) and (18.16). These are given in column F of Table 18.9. At once it is seen that by defining the available food in a less restricting way we have obtained reasonable values of W_∞ even with zero fishing mortality. Moreover, they do not differ greatly—except at very high values of F—from the series found in §18.4.1 for plaice (reproduced in column (c) of Table 18.9 for comparison) obtained by relating linearly the pre-war and war-time values of L_∞ to estimates of the corresponding biomass (hypothesis (b)). The resulting curve of $Y_{W'}/R$ as a function of F for hypothesis (e) is shown in Fig. 18.11, curve (e), and will be discussed in §18.4.2.5.

Although we find that hypothesis (e) gives a reasonable degree of change in growth with population density, it has certain implications which do not accord with reality as closely as might be desired. The principle objection is that the total food available per year is taken as being unaffected by whatever amount is consumed by the fish population.

This has the corollary that the food consumption of a fish is limited by its 'appetite' and by the local density of food on the sea-bed, but is in no way influenced by the feeding activity of other fish competing for the same supply.

18.4.2.4 *Hypothesis* (f_1)

We suggested in §9.4.3.2.3 that the above anomaly might be resolved by introducing the concept of the grazing power of the fish population and taking some account of the dynamics of the food populations (hypothesis (f)). This leads to more complex theoretical models than do the previous hypotheses, but in that sub-section we suggested certain simplifying assumptions which could be made when the available data were limited. In attempting to apply these simplified methods to North Sea plaice, the main difficulty is that it is not the only fish predatory on the species of food organisms which comprise its food; the dab (*Pleuronectes limanda* L.), is probably the main competitor, the whiting (*Gadus merlangus* L.) and the turbot (*Rhombus maximus* L.) being minor ones (Todd, 1905). It would be desirable to view the problem as one of predatory balance within a community, and deal with it, for example, by methods such as those outlined in §11.2.1, but at the present time there is insufficient quantitative information about the competitors with the plaice for this to be practicable. However, all the species mentioned above are caught by the same type of gear, and the indications are that the major changes in fishing intensity that have occurred in the past have affected all of them. As a working basis we shall therefore regard the behaviour of the plaice population as approximating to that of the competing species, so that simpler methods are applicable.

In these circumstances (9.38) can be used to give the annual food consumption of the plaice population, and dividing both sides by R, the annual food consumption per plaice recruit becomes

$$\frac{\Xi}{R} = \frac{r\omega}{R}\left(1 - e^{-G\lambda'}\right) \quad .. \quad .. \quad .. \quad .. \quad (18.17)$$

Now this equation can be regarded as containing only two unknown parameters, i.e. $r\omega/R$ and $G\lambda'$, and these may be estimated if data for two levels of population abundance and growth rate are available. It will be remembered from §9.4.3.2.3 that if the population in question can be taken as comprising the constant fraction x of all competing populations, then we have approximately

$$\frac{r\omega}{R} \equiv \frac{xr\omega}{R}$$

and

$$G\lambda' \equiv \frac{G\lambda'}{x}$$

Since in the following it is not necessary to estimate the individual parameters r and ω, or G and λ', there is no purpose in writing (18.17) in the form containing x explicitly, but the above relationships should be borne in mind when interpreting the values of $r\omega/R$ and $G\lambda'$ which will be presented.

A value of Ξ/R and Ξ_L/R for each level of abundance can be computed by means of (18.13) and (18.15). The ratio of the grazing mortalities is then defined by the equation

$$\frac{{}_2G}{{}_1G} = \frac{{}_2\Xi\left(1 - \dfrac{{}_2\Xi}{{}_2\Xi_L}\right)}{{}_1\Xi\left(1 - \dfrac{{}_1\Xi}{{}_1\Xi_L}\right)} = {}_2u_1$$

From this and (18.17) we obtain the pair of simultaneous equations

$$\frac{{}_1\Xi}{R} = \frac{r\omega}{R}\left(1 - e^{-{}_1G\lambda'}\right) \quad .. \quad .. \quad .. \quad .. \quad (18.18)$$

$$\frac{{}_2\Xi}{R} = \frac{r\omega}{R}\left(1 - e^{-{}_2u_1\,{}_1G\lambda'}\right) \qquad \tag{18.19}$$

which provide, by trial, a solution for ${}_1G\lambda'$ and hence for $r\omega/R$.

The two levels of growth and density of plaice for which data are available relate to the pre-war steady state and the period during the 1939-45 war, these being used to define the parameters of hypothesis (b) in §18.4.1. For *hypothesis* (f_1) we use the same data to define values of ${}_1G\lambda'$ and $r\omega/R$. In §16.4.1.1 it was shown that the value of W_∞ for the war period was 1982 gm. and that the average war-time biomass was probably at least three times that maintained before the war. Now the latter, estimated in terms of biomass per recruit from (5.8), is 266 gm., so that the average war-time value of $\bar{P}_W/R$ can be taken as about 800 gm. With $W_\infty = 1982$ gm. such a value of $\bar{P}_W/R$ corresponds to a fishing mortality of 0.27; in other words we can *for this purpose* take the war period as equivalent to a steady state with $F = 0.27$ throughout. For hypothesis (f_1) the two levels of growth and density are therefore specified by:

$$F = 0.73;\ W_\infty = 2867 \text{ gm.}$$

$$F = 0.27;\ W_\infty = 1982 \text{ gm.}$$

and by means of (18.12) and (18.14) we obtain

$$\frac{{}_1\Xi}{R} = 1122 \text{ M-g-es.}\ ;\ \frac{{}_1\Xi_L}{R} = 1471 \text{ M-g-es.}$$

$$\frac{{}_2\Xi}{R} = 2800 \text{ M-g-es.}\ ;\ \frac{{}_2\Xi_L}{R} = 3856 \text{ M-g-es.}$$

Inserting these values into (18.18) and (18.19) gives the estimates

$${}_1G\lambda' = 0.160$$

$$\frac{r\omega}{R} = 7587 \text{ M-g-es.}$$

We shall comment on the implications of these particular values below; here we continue with the calculation of the curve of Y_W/R for hypothesis (f_1), the essential step being to compute the values of W_∞ corresponding to those of F listed in column A of Table 18.9. This may be done graphically with sufficient accuracy, as follows.

For any specified fishing mortality F and corresponding growth parameter ${}_xW_\infty$, the annual food consumption per recruit is given from (9.41) as

$$\frac{{}_x\Xi}{R} = \frac{r\omega}{R}\left(1 - e^{-{}_xu_1\,{}_1G\lambda'}\right) \qquad \tag{18.20}$$

where

$${}_xu_1 = \frac{{}_x\Xi\left(1 - \dfrac{{}_x\Xi}{{}_x\Xi_L}\right)}{{}_1\Xi\left(1 - \dfrac{{}_1\Xi}{{}_1\Xi_L}\right)}$$

and in which $r\omega/R$ and ${}_1G\lambda'$ are now known. For each value of F we take a series of values of W_∞ and use them to calculate ${}_1\Xi/R$ and ${}_1\Xi_L/R$ from (18.13) and (18.15). Putting these into the right-hand side of (18.20) enables another series of estimates of Ξ/R, say ${}_2\Xi/R$, to be computed. Each of these two series of values, ${}_1\Xi/R$ and ${}_2\Xi/R$, is plotted against W_∞, and the value of the latter at the point of intersection of the two curves is that which satisfies both sides of (18.20), and is therefore the one required for that fishing mortality. In this way we obtain the series of W_∞ given in column G of Table 18.9, which are similar to those of hypothesis (e) over the middle range of F but are much lower at low values and do not increase as rapidly for F greater than 0.73. These are the general characteristics to be expected as a result of allowing for competitive grazing among the predators.

18.4.2.5 *Analysis of yield curves—hypotheses* (f_2) *and* (f_3)

We must now investigate the properties of the yield curves resulting from hypotheses (e) and (f_1). Values of Y_W/R can be calculated by means of (4.4) in the usual way, using the estimates of W_∞ given in columns F and G of Table 18.9, and obtaining first the value of t_0 corresponding to each value of W_∞ from (18.7) with $t_{\rho'} = 3.72$ years and $W_{\rho'} = 122.9$ gm. as before. The results are plotted in Fig. 18.13 (curves (e) and (f_1)), together with curve (a) for a constant W_∞ of 2867 gm. and that derived by fitting a straight line to the observed pre-war and war-time values of $\bar{P}_W$ and L_∞ (curve (b)). As some of these yield curves appear nearly coincident over parts of their range when plotted, values of Y_W/R from which they are drawn are given in Table 18.10.

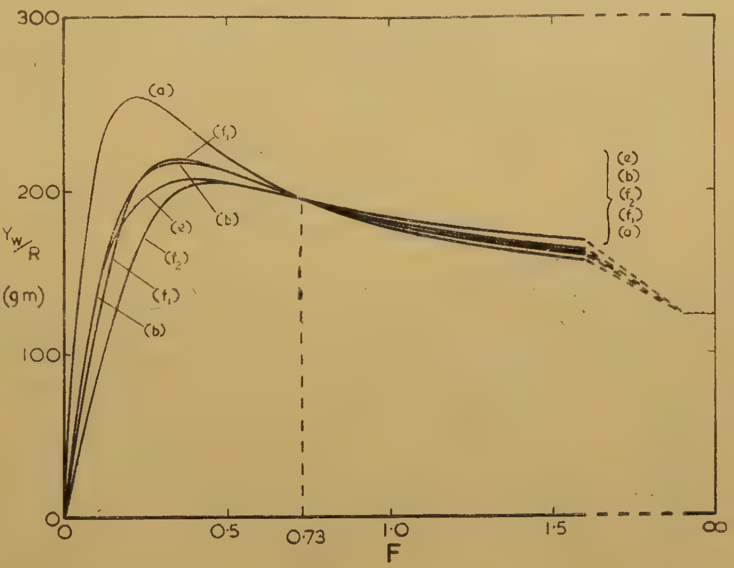


FIG. 18.13
PLAICE:
GROWTH VARYING WITH FOOD SUPPLY AND CONSUMPTION

[Yield per recruit, Y_W/R, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.2); curve (b) L_∞ varying linearly with $\bar{P}_W/R$ (Fig. 18.9); curves (e), (f_1) and (f_2) growth varying with food supply and consumption according to hypotheses developed in §9.4.3. As curves (b), (e) and (f_1) are nearly coincident over parts of their range the data from which they have been drawn are given in Table 18.10, p. 493. Values of W_∞ for each value of F are given in Table 18.9. Curve (f_1), incorporating the effect of grazing by the fish population on the food organisms, is expected to be the most realistic, and its close similarity to curve (b) based on an empirical density dependent relation is worthy of note.]

It will be seen at once that all three curves (b), (e) and (f_1) differ appreciably from curve (a), notably in that the positions of $(F)_{\max}$ are farther to the right and the yield maxima are lower. Curves (b) and (f_1) are the most similar, being virtually indistinguishable for values of F greater than 0.15; curve (e), though broadly similar to these, has the least pronounced maximum and is above all the others at high values of F. On the whole, however, the differences between the curves of Fig. 18.13 are not great, except at low values of F (for example, the yield predicted from curve (a) at $F = 0.05$ is nearly twice as great as that from any of the other curves). It therefore appears that the annual yield is relatively insensitive to variations of growth with density over a wide range of fishing mortality; in particular, the close similarity between curves (b) and (f_1) suggests that the procedure of relating estimates of L_∞ linearly to biomass (hypothesis (b)) is, in the plaice, a good second best to using the more complex model based on hypothesis (f_1), which latter we must regard as our best representation of the density dependence of growth in this species. We shall accordingly take hypothesis (b) to relate growth and density in plaice in certain later calculations of this paper, when hypothesis (f_1) would be particularly intractable; though our most recent investigations suggest that for some purposes a linear relationship between L_∞ and population numbers, $\bar{P}_N$, may be even more satisfactory and certainly simpler to handle (see §18.4.2.6). In many cases, however, particularly in the calculations of §19, even the use of hypothesis (b) proves tedious, and it is worth noting that curve (a) with W_∞ constant throughout at 2867 gm. does not differ so much from curve (b) as to invalidate its use completely, except when very low values of F are involved.

Some idea of the possible range of effect that can result from intraspecific competition for food in an exploited fish population can be gained from hypothesis (f), by taking values of growth and density other than those observed during the war period. The most interesting case is that in which the food supply is so limited that when the population density is at its greatest (i.e. when there is no fishing) there is sufficient food for maintenance purposes only. We shall call this *hypothesis* (f_2), implying that fish remain throughout life at the weight at which they are recruited, i.e. $W_r = W_{\rho'} = 122.9$ gm. At low values of F this therefore represents the phenomenon of stunted growth in its extreme form, and the two levels of growth and density are specified by the values

$$F_1 = 0.73 \; ; {}_1W_\infty = 2867 \text{ gm.}$$

$$F_2 = 0 \quad ; {}_2W_\infty = 122.9 \text{ gm.}$$

Proceeding as for hypothesis (f_1), we obtain

$${}_1G\lambda' = 0.301$$

$$\frac{r\omega}{R} = 4322 \text{ M-g-es.}$$

and the estimates of W_∞ given in column H of Table 18.9. The drastic reduction in growth at all low values of F is apparent, but despite this the corresponding curve of $Y_{W'}/R$ shown in Fig. 18.13 (curve (f_2)) still has a definite maximum and differs appreciably from the others only for values of F less than about 0.4.

At the other extreme we have the case of growth being independent of population density, and it is interesting to find that this is not inconsistent with the concept of grazing we have developed. Thus for *hypothesis* (f_3) we can put $W_\infty = 2867$ gm. at both $F = 0.73$ *and* zero, so that the two levels are specified by

$$F_1 = 0.73 \; ; {}_1W_\infty = 2867 \text{ gm.}$$

$$F_2 = 0 \quad ; {}_2W_\infty = 2867 \text{ gm.}$$

giving the values

$${}_1G\lambda' = 0.008$$

$$\frac{r\omega}{R} = 140{,}300 \text{ M-g-es.}$$

The values of W_∞ at intermediate fishing intensities differ only very slightly from 2867, and the corresponding curve of $Y_{W'}/R$ for hypothesis (f_3) is virtually identical with curve (a). The fact that a positive value of $G\lambda'$ is obtained in these circumstances suggests that the possibility of *decreases* in growth rate with decreased density should not be ruled out, since a value of $G\lambda'$ less than 0.008 would result in a value of W_∞ greater than 2867 at $F = 0$. The phenomenon arises because changes in the age-composition of the population alter both its grazing power and maintenance requirements, but not in the same proportion. The effect is of course slight, and might only be expected where food is extremely abundant relative to the size of the fish population subsisting on it.

Curves (a) and (f_2) of Fig. 18.13 therefore illustrate two extreme possibilities for the effect of density on growth in plaice, with curve (f_1) as the best assessment of it within the limits of the available data. It would be misleading, however, to regard curves (a) and (f_2) as in any sense giving probable limits for the density dependent growth effect; the probable range within which lies the true curve is certainly much narrower than that bounded by curves (a) and (f_2). Thus we showed in §16.4.1.1 that the war-time growth of plaice was significantly lower than the pre-war growth, but hypothesis (f_2) would require the value of W_∞ corresponding to the three-fold increase in biomass that was observed during the war to be about 600 gm. Inspection of the data in Table 16.10 indicates how extreme this requirement is. It will be appreciated that limiting curves of Y_W/R, with which are associated fairly definite probabilities, could be constructed from a knowledge of the variance of the values of W_∞ for the war period given in that table.

18.4.2.6 *Critical comparison of hypotheses and some implications*

Despite the proximity of the yield curves in Fig. 18.13 over much of their range, the biological implications of the hypotheses are very different and further examination of them leads to some conclusions of general interest. A better discrimination between the various hypotheses than can be obtained from that figure is provided by the corresponding curves of biomass, equivalent to the catch per unit effort with a 70 mm. mesh. These are shown in Fig. 18.14 with the same lettering as before, and it can be seen that the predicted biomasses at low values of F do indeed differ considerably. It is of special interest that curves (f_1) and (f_2) are inflected. This is a feature not encountered with any of the models examined previously, nor does it occur in curves (b) and (e), although they both take some account of the variation of growth with density. The deduction from hypothesis (f) of a characteristic sigmoid curve of stock weight follows primarily from the grazing mechanism incorporated in it. At the highest densities this model can result (according to the magnitude of the grazing parameter) in grazing being so severe that a large part of the availablefo od is consumed each year, so that any increase in the number of fish due to a decrease in fishing merely results in nearly the same amount of food being shared between more fish. Consequently, growth decreases more or less in proportion and the biomass stays nearly constant. As would be expected, the effect is most pronounced with curve (f_2) where the postulated change of growth with density implies a relatively sparse food supply and higher grazing mortalities than in hypothesis (f_1). From what is known of growth in dense fish populations (see §9.4.1) this behaviour seems entirely plausible and is, in fact, what might be anticipated under conditions of severe competition for a limited supply of food.

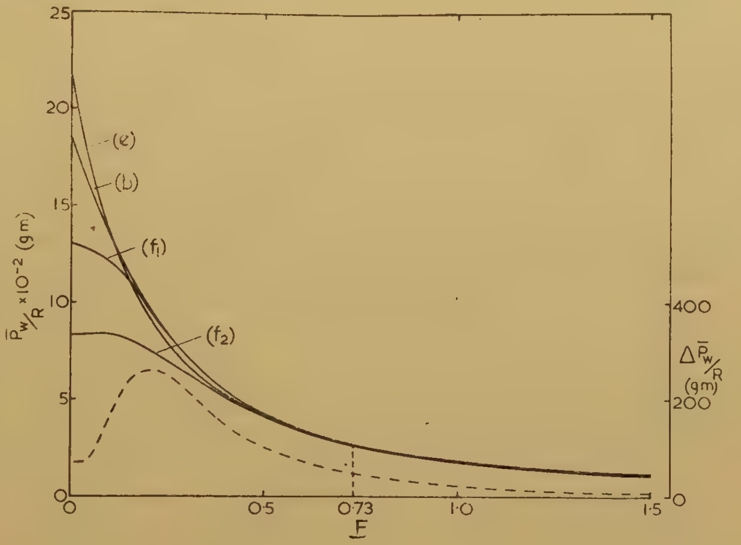


FIG. 18.14
PLAICE:
GROWTH VARYING
WITH FOOD SUPPLY
AND CONSUMPTION

[Curves of total biomass per recruit, $\bar{P}_W/R$, corresponding to yield curves (b), (e), (f_1) and (f_2) of Fig. 18.13. Incorporating a grazing mechanism causes the biomass curve to be inflected ((f_1) and (f_2)). The broken line is the first differential of curve (f_1), with ordinates given on the right hand scale, and has a bearing on the sigmoid curve theory (see text).]

Now, the 'sigmoid curve theory' of population growth (see §17.8) can give rise to an inflected curve of biomass against F, and it is interesting to find this feature in the most realistic of the analytical models we have examined so far. Both curves (f_1) and (f_2) of Fig. 18.14 are markedly asymmetrical. Their first differentials, which, according to one version of that theory, should approximate to the curve of steady yield as a function of fishing mortality, have maxima at about $F = 0.2$. The differential form of curve (f_1) is shown by the broken line in Fig. 18.14, and comparison with the true yield curve (f_1) of Fig. 18.13 shows that although the maxima occur at fairly similar fishing mortalities the maximum height of the former is much exaggerated relative to the height at $F = 0.73$.

We have pointed out above that the sigmoid shape of the $\bar{P}_W/R$ curves (f_1) and (f_2) is due to the particular inter-relations postulated between growth, population numbers and biomass. It is instructive to examine the relationships between L_∞ and these two measures of population density, predicted by the various hypotheses we have been considering. Because of differences in character between the growth and density data in plaice and haddock, it was found convenient to adopt a different empirical relationship in each, L_∞ being taken as a linear function of biomass ($\bar{P}_W$) for the plaice and of population numbers ($\bar{P}_N$) for the haddock. We now show that it is possible to establish which of these functions is the more satisfactory for general use in theoretical models.

For each value of fishing mortality, L_∞ can be computed directly from values of W_∞ given in Table 18.9. Since, with the mesh in use before the war, there is no pre-exploited phase in plaice, changes in growth cannot affect $\bar{P}_N/R$ (through changes in $t_{\rho'}$), and the corresponding values of this characteristic are therefore those already plotted in Fig. 17.5.

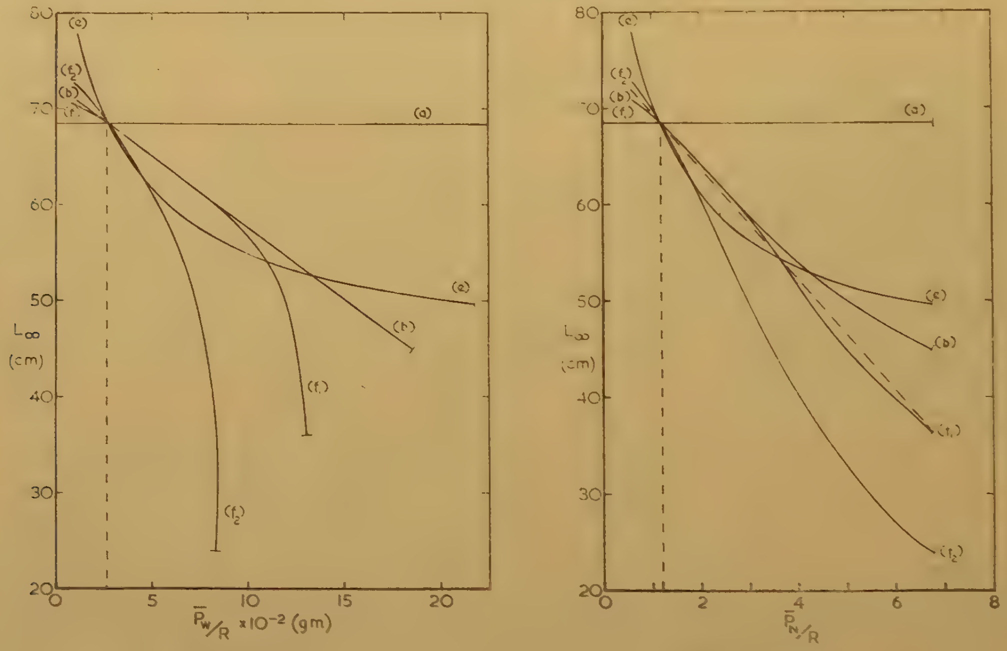


Fig. 18.15.1

Fig. 18.15.2

FIGS. 18.15 PLAICE: DENSITY DEPENDENT GROWTH

[Relationships between growth and density predicted by the hypotheses incorporated in the yield curves of Fig. 18.13. In these figures changes in density are caused by changes in fishing mortality, and the curves are terminated at the density in the virgin stock predicted by the hypothesis in question.]

Fig. 18.15.1 Relationships between L_∞ and biomass per recruit, $\bar{P}_W/R$. The vertical broken line is at the mean pre-war biomass, corresponding to a value of $F = 0.73$. Curves (b) and (f_1) are virtually coincident up to about four times the pre-war biomass, but diverge beyond.

Fig. 18.15.2 Relationships between L_∞ and population numbers per recruit, $\bar{P}_N/R$. The vertical broken line is at the mean pre-war value of $\bar{P}_N/R$ corresponding to $F = 0.73$. Curves (b) and (f_1) are nowhere quite so close as in Fig. 18.15.1, but do not diverge nearly as much at high densities. The sloping broken line shows how closely curve (f_1) could be represented by an appropriate linear regression of L_∞ on $\bar{P}_N/R$.

The resulting curves of L_∞ against $\bar{P}_W/R$ are shown in Fig. 18.15.1, and against $\bar{P}_N/R$ in Fig. 18.15.2, with the same lettering as before. Curve (b) of Fig. 18.15.1 is, of course, linear by definition, and is closely linear in Fig. 18.15.2, but especially interesting is the finding that hypothesis (f_1) (with a moderate grazing intensity) gives curves of L_∞ against both $\bar{P}_W/R$ and $\bar{P}_N/R$ that are virtually indistinguishable from straight lines over a wide range of density. Thus the (f_1) curves begin to depart appreciably from linearity only above a value of $\bar{P}_W/R$ of about 1000 gm. and a $\bar{P}_N/R$ of about 4, corresponding in each case to a value of F of roughly 0.1. In contrast, both the (e) lines show pronounced curvature over the whole range of density. The steep fall in curves (f_1) and (f_2) of Fig. 18.15.1 at high densities is, of course, due to the same mechanism as that which produces the sigmoid shape of the $\bar{P}_W/R$ curves given by this hypothesis, and in this figure the curves terminate at the maximum possible values of $\bar{P}_W/R$ (i.e. with $F = 0$) predicted by each hypothesis.

It can be concluded, therefore, that postulating a linear relationship between L_∞ and biomass gives a satisfactory representation of the density dependence of growth in plaice up to a density some four times the pre-war level and about three-quarters of that in the virgin stock, i.e. down to a value of F of about 0.2. A linear relationship between L_∞ and population numbers is not much inferior over this range and has the advantage that it can probably be safely extrapolated over a wider range of density. It should be mentioned however that, strictly, these relationships hold only for changes in density caused by changes in fishing mortality and have no more general significance. Nor for that matter has any relationship between growth and density, whether observed or deduced. This is because, in terms of our theoretical models, a given value of $\bar{P}_W$ or $\bar{P}_N$ can result from widely differing age-compositions and growth rates, each of which will produce different estimates of total food consumption, grazing power, etc., since these characteristics depend on the size-composition of the population (see §17.8). For this reason care would have to be taken in applying any function relating L_∞ and $\bar{P}_N$ found by considering changes in F to, say, an investigation of the effects of large changes in mesh size, especially at high fishing intensities. Similarly, a relationship deduced from density changes due to fluctuations in recruitment is not strictly comparable with one based on changes in fishing mortality. The discrepancy would probably be slight, however, and the observation that estimates of L_∞ in the haddock are linearly dependent on population numbers over a range covering a five-fold density change (see §16.4.1.2, Fig. 16.13) seems to be compelling evidence in support of hypothesis (f) and the model based upon it.

Some further deductions from the (f) hypotheses concern the predicted ratios of the mean standing crops of the food organisms and the predatory fish populations; these are relevant to the results of practical investigations on the relative biomasses of populations on adjacent levels of a food-chain, and provide a further discrimination between (f_1), (f_2) and (f_3). Since plaice are not the only species predatory on the food organisms in question we must interpret (18.17) as

$$\frac{\Xi}{R} = \frac{xr\omega}{R}\left(1 - e^{-G\lambda'/x}\right) \qquad .. \qquad .. \qquad (18.21)$$

where x is the fraction that plaice comprise of the total predators. Now the biomass of the food organisms can be computed from (5.8) using the previously estimated food consumption of plaice and the grazing mortality coefficient they generate, i.e.

$$\bar{p}_W = \frac{\Xi}{G}$$

The total biomass of predatory fish is $\bar{P}_W/x$, where $\bar{P}_W$ is the biomass of plaice, and hence the ratio we require is

$$\frac{\Xi}{G} \times \frac{x}{\bar{P}_W}$$

This can be written in terms of the food consumption and biomass per plaice recruit without altering its value, as

$$\frac{\Xi}{RG} \times \frac{xR}{\bar{P}_W} \qquad \ldots \quad \ldots \quad \ldots \quad \ldots \qquad (18.22)$$

For the pre-war state we have found $\bar{P}_W/R = 266$ gm., and hypothesis (f_1) gives the value of $G\lambda'$ (which is equivalent to the quantity $G\lambda'/x$ in (18.21)) of 0.16. Hence (18.22) becomes

$$\frac{\Xi}{R} \times \frac{R}{266} \times \frac{\lambda'}{0.16}$$

and the ratio is independent of the factor x. We have no definite knowledge of the effective life-span of the food organisms, but a reasonable value of λ' might be 1 year, bearing in mind that it still includes any mortality due to causes other than predatory grazing. With Ξ/R equal to 1122 M-g-es. for the pre-war state, the ratio of total prey to total predators for this period predicted by hypothesis (f_1) is therefore

$$\frac{1122}{266 \times 0.16} = 26$$

We found previously that by comparing the war-time growth predicted by each of the (f) hypotheses it was clear that hypothesis (f_2) resulted in a value of W_∞ which was much smaller than the observed values, although the difference in the case of hypothesis (f_3) was not so marked. On the other hand, the above method of comparing the hypotheses shows the extreme implications of hypothesis (f_3) better than it does those of hypothesis (f_2), since using the values of $G\lambda'$ found for the latter hypothesis gives a prey-predator ratio of

$$\frac{1122}{266 \times 0.301} = 14$$

This is about half that predicted from hypothesis (f_1), whereas hypothesis (f_3) predicts a ratio

$$\frac{1122}{266 \times 0.008} = 525$$

which is enormously greater. In other words, although the war-time growth was not greatly different from that before the war, the small difference has nevertheless profound implications as far as the relative abundance of predators and prey is concerned. Clearly, both hypotheses (f_2) and (f_3) must be regarded as very extreme formulations of the density dependence of growth, and it is reasonable to suppose that the true yield curve lies nearer to curve (f_1) of Fig. 18.13 than to either curves (f_2) or (a).

18.5 TWO FACTORS VARYING SIMULTANEOUSLY WITH POPULATION DENSITY

In §§18.2 to 18.4 we have investigated separately the effects of dependence on population density of natural mortality and growth in plaice, and of recruitment and growth in haddock. It will be remembered that whereas the separate variation of either natural mortality or growth in the way we have considered in plaice each tends to increase $(F)_{\max}$ and reduce $(Y_W/R)_{\max}$, the variation of recruitment and of growth in haddock have opposing effects. In §§18.5.1 and 18.5.2 respectively, the effects of their simultaneous variation with density are analysed, the necessary population models going a little further toward reproducing the complete inter-dependence of factors that occurs in nature.

18.5.1 *Natural mortality and growth in plaice*

The natural mortality of plaice has been taken to vary linearly with population numbers (§18.2), and for the density dependence of growth we shall assume hypothesis (b) (§18.4.1), in which L_∞ is a linear function of population biomass. We can therefore use the series of M given in Table 18.3 (column F) and reproduced in column B of Table 18.10 to calculate the required estimates of W_∞ for each value of F, since $t_{\rho'}$ is constant in this case, and M is independent of W_∞ (the converse is not true, since M appears in the equation for $\bar{P}_W$). In all other respects the calculation is similar to that for hypothesis (b) and results in the series of W_∞, given in column C of Table 18.11. The solution was actually obtained by the iterative method, but it could equally well have been reached graphically using, for each value of F, the appropriate value of M from Table 18.3. Compared with the series of W_∞ obtained from hypothesis (b) (column C of Table 18.9), it will be seen that there is a smaller range of W_∞, since at this stage the effect of the density dependence of M is simply to restrict the range of $\bar{P}_W$.

After first finding the corresponding series of t_0 as before, we can calculate the curve of Y_W/R as a function of F from (4.4) in the usual way, using the values of M and W_∞ given in columns B and C of Table 18.11. This is shown as curve (n) of Fig. 18.16. Shown, also, for comparison, is curve (a) with W_∞ and M constant, curve (b) with W_∞ varying as in hypothesis (b) and $M = 0.1$ (constant), and curve (m) in which M alone varies and W_∞ is constant at 2867 gm. (Fig. 18.3). The joint density dependence of M and W_∞ is seen to be additive, in that $(F)_{\max}$ and $(Y_W/R)_{\max}$ are greater and less respectively for curve (n) than for any of the other three curves. However, curve (n) still has a well defined maximum—at $F \simeq 0.4$—and the same general shape; in fact, with fishing mortalities above 0.73 all the curves are so similar that only the two extreme ones, (a) and (n), and the middle one, (m), can be shown.

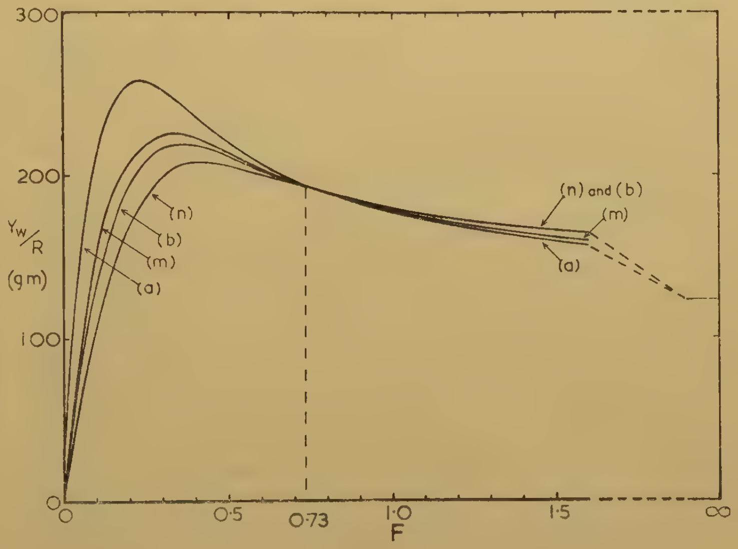


FIG. 18.16 PLAICE: NATURAL MORTALITY AND GROWTH SIMULTANEOUSLY DENSITY DEPENDENT

[Yield per recruit, Y_W/R, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.2); curve (m) density dependent natural mortality (Fig. 18.3); curve (b) density dependent growth (Fig. 18.8); curve (n) density dependent natural mortality and growth. With both factors density dependent the height of the maximum is lower, and the value of $(F)_{\max}$ higher, than with either factor alone density dependent. See also Table 18.11.]

It will be appreciated that the above result could not readily have been foreseen, since the effect on yield of M varying with density simultaneously with growth is complex. Thus it could apparently have been argued that although if fishing is reduced, for example, the resulting increase in natural mortality would tend directly to reduce the yield, at the same time it would tend, indirectly, to increase it, through the lower density enhancing the growth rate. Clearly, such argument must be inconclusive.

18.5.2 *Recruitment and growth in haddock*

The calculations involved when both recruitment and growth vary with population density are the most difficult that we have attempted; nevertheless, the results obtained have a special interest because a self-regenerating model allowing for the density dependence of growth should give a fair representation of an exploited fish population.

Computation is by a direct extension of the iterative methods described earlier and combines those of §§18.3.2 and 18.4.1. In addition to the equations for γ, $t_{\rho'}$, W_∞ and $\bar{P}_N/R$ given previously [(18.4), (18.8), (18.9) and (18.11) respectively], the following relationships are required:—

$$\bar{P}_N = \frac{\bar{P}_N/R}{\alpha}\left(1 - \frac{\beta}{\gamma}\right) \quad \ldots \quad (18.23)$$

$$L_\infty = a + b\bar{P}_N \quad \ldots \quad (18.24)$$

and

$$t_0 = t_\rho + \frac{1}{K}\log\left\{1 - \frac{L_\rho}{L_\infty}\right\} \quad \ldots \quad (18.25)$$

Since L_∞ is related linearly to population numbers in absolute units in (18.24) it is necessary to obtain an independent estimate of the coefficient b by dividing the value of bR used in §18.4.1 by the mean pre-war haddock recruitment given in §15.2.2, i.e.

$$b = \frac{-2.636}{8.5 \times 10^8} = -3.101 \times 10^{-9}$$

All the remaining parameters in the above equations take their usual values (see §§18.3.2 and 18.4.1). In particular, the values of α and β are those listed on page 273 (see Fig. 15.15) and used to construct the yield curves of Figs. 18.6 and 18.7 in which the growth parameters are constant.

We have investigated the behaviour of yield with changes in both fishing mortality and mesh-size (i.e. in $L_{\rho'}$) but the procedure is the same in each case and the following description will suffice for both calculations. The iterative process is started by taking the values of γ, for each value of F and $L_{\rho'}$, that were obtained in §18.3.2; these we refer to as our first estimates and denote by ${}_1\gamma$. We also calculate first estimates of $\bar{P}_N/R$ from (18.11), denoting them by ${}_1(\bar{P}_N/R)$, and these two quantities, ${}_1\gamma$ and ${}_1(\bar{P}_N/R)$, contain the usual values of W_∞, $t_{\rho'}$, and t_0 which can similarly be regarded as first estimates. From (18.23) it is then possible to compute ${}_1(\bar{P}_N)$ for each value of F and $L_{\rho'}$ and for each pair of values of α and β. We now have first estimates of all the quantities defined by the equations listed above and can proceed to a calculation of the second estimates. Thus putting the estimates ${}_1(\bar{P}_N)$ into (18.24) we obtain ${}_2L_\infty$, and hence, from (18.8), (18.9) and (18.25) values of ${}_2t_{\rho'}$, ${}_2W_\infty$ and ${}_2t_0$. We now come to the longest stage in the iterative cycle—that of calculating the second estimates ${}_2\gamma$, the equation for which will contain ${}_2t_0$, ${}_2t_{\rho'}$, and ${}_2L_\infty$, and hence revised values of H, h, and J (see §18.3.2). To complete the second cycle we compute ${}_2(\bar{P}_N/R)$ and hence ${}_2(\bar{P}_N)$, and the whole process is repeated until either successive estimates of the various parameters do not differ appreciably, or a sufficient number of them have been obtained for their limiting values to be found graphically or by difference methods.

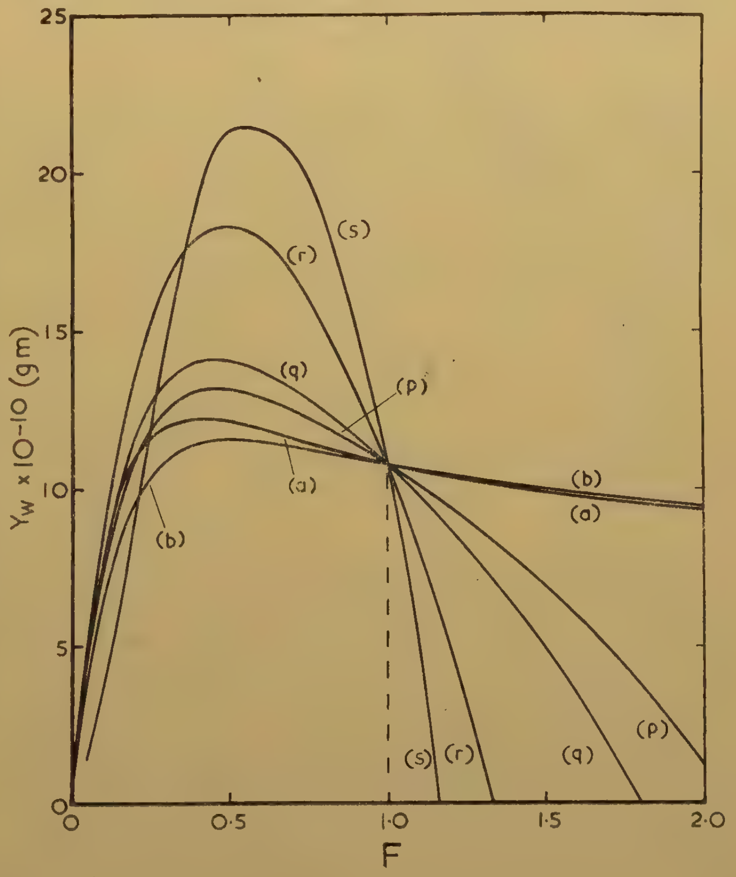
The first results to examine are the final estimates of R and W_∞ corresponding to various values of F and mesh size, since these are the primary variables whose dependence on density we are considering. They are given in Tables 18.12 and 18.13 for the first four pairs of α and β (shown at the top of each column). Also tabulated are the corresponding values of $t_{\rho'}$, since although this parameter depends on W_∞ it has a direct effect on the yield by determining the span of the exploited phase (cf. §18.4.1). As would be expected, the high values of R are associated with low values of W_∞ and vice-versa. With the higher values of β we also find two features met previously, but not together in one population model. The first is that at certain high values of F and small mesh sizes, R falls to zero, and the population becomes extinct, as found in §18.3.2 when recruitment alone varied with density. This is shown in the tables by a zero entered at the appropriate value of F or mesh, the corresponding value of W_∞ always being 1495 gm., i.e. the constant a of (18.24) (56.88 cm.) converted to weight. The second feature is that with low values of F and large meshes the growth rate becomes so low that fish cannot become large enough during their lives to be retained by the mesh in question; in other words, the value of $t_{p'}$ is found to be greater than t_λ, or it may even be that L_∞ is less than $L_{p'}$.

Only the four lowest values of β appear in the above tables, because with the fifth pair of values of α and β ($\alpha = 0.085 \times 10^{-9}$, $\beta = 16{,}000$; curve (t) of Figs. 18.6 and 18.7) the points of extinction and those at which $t_{p'} = t_\lambda$ are too near to the pre-war values of F and mesh size to make computation of the yield curves worth-while. Indeed, even with $\beta = 13{,}000$ [curve (s)] these points are reached with meshes of only some 10 mm. below or above the pre-war mesh, as can be seen from Table 18.13. Some implications of this result are discussed later in this section.

We next investigate the effect of these correlated changes in recruitment and growth on the yield. For this purpose values of Y_W/R are computed from (4.4) for each value of F and mesh size, using the final estimates of W_∞, $t_{p'}$ and t_0. The actual yield can then be found by multiplying Y_W/R by the appropriate value of R in Table 18.12. The resulting yield curves are shown in Figs. 18.17 and 18.18, for each of the four pairs of α and β under investigation [curves (p) to (s)]. For comparison are shown curves with all parameters constant [curve (a)] and with recruitment constant but growth varying with density [curve (b)]; these are computed from the corresponding curves of Y_W/R shown previously (Figs. 17.24 and 18.10), by multiplying by $R = 8.5 \times 10^8$.

FIG. 18.17
HADDOCK:
RECRUITMENT AND
GROWTH DENSITY
DEPENDENT

[Absolute yield, Y_W, as a function of F with a 70 mm. mesh. Curve (a) constant parameters (Fig. 17.24); curve (b) recruitment constant, growth density dependent (Fig. 18.10); curves (p) to (s) recruitment and growth density dependent, incorporating the relations between recruitment and egg-production shown in Fig. 15.15 and values of α and β given on p. 273. Comparison of curves (p) to (s) with those of the same lettering in Fig. 18.6 shows the compensating effect of a density dependent growth. Curve (s) is unique in that it is the only yield curve in this paper the ascending limb of which is concave. Note that curves (p) to (s) imply extinction at certain high values of F. See also Table 18.12.]



Taking first the variation of yield with respect to F (Fig. 18.17), it is seen that even when recruitment is little affected by density changes (curve (c), see Table (18.12)) $(Y_W)_{\max}$ is increased to a value greater than that in curve (a) and thus the effect of the dependence of growth on density (curve (b)) is outweighed. This latter, however, depresses the maximum greatly compared with $(Y_W)_{\max}$ for the same α and β shown in Fig. 18.6 with growth constant. This is especially noticeable with the higher values of β; thus

$(Y_W)_{\max}$ of curve (s) in Fig. 18.6 is about 43×10^{10} gm., but in the corresponding curve of Fig. 18.17 it is only half that value. There are also interesting changes in the value of $(F)_{\max}$ as recruitment is made to increase more rapidly with density. Curves (b) to (s), in all of which growth is density dependent, form a series in which $(F)_{\max}$ first decreases and then increases again as β increases. It is never as low as in curve (a), however, nor therefore as in the curves of Fig. 18.6 where the effect of the variation of recruitment alone is to make $(F)_{\max}$ lower still. The extinction points in Fig. 18.17 are almost identical with those in Fig. 18.6. This means that the harmful effect of rapid growth at very low densities in causing fish to be retained by the gear at a lower age is just counteracted by the increased fecundity to which it gives rise. It will be noted also that curve (s) does not quite reach the origin, since at values of F lower than 0.05 we have found $t_{\rho'} > t_\lambda$ with a 70 mm. mesh (see above); in fact, the model ceases to be valid in this range of F.

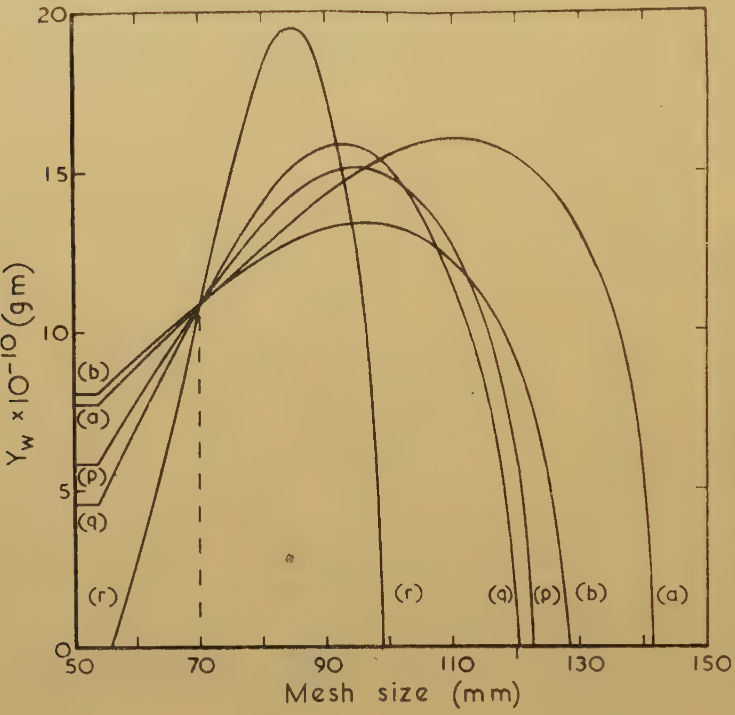


FIG. 18.18
HADDOCK:
RECRUITMENT AND
GROWTH DENSITY
DEPENDENT

[Absolute yield, Y_W, as a function of mesh with $F = 1.0$. Curve (a) constant parameters (Fig. 17.25); curve (b) recruitment constant, growth density dependent (Fig. 18.12); curves (p), (q) and (r) recruitment and growth density dependent as in Fig. 18.17. Comparison with Fig. 18.7 shows the compensating effect of a density dependent growth. Note that curves (p), (q) and (r) imply extinction with certain small meshes. See also Table 18.13.]

More or less parallel changes are seen in the yield-mesh curves of Fig. 18.18 which correspond to those shown in Fig. 18.17 except that curve (s) is absent. $(Y_W)_{\max}$ increases as β increases, but is only about half that in the corresponding curve of Fig. 18.7. However, the size of mesh giving the maximum yield is affected much more than is $(F)_{\max}$ in Fig. 18.17, the reduction being especially marked in curve (r). The mesh at which the yield becomes zero because $t_{\rho'} > t_\lambda$, is also reduced. Extinction occurs only with curve (r), and at nearly the same mesh size as in the corresponding curve of Fig. 18.7.

Fig. 18.19 shows the variation of catch per unit effort, $\bar{P}'_W$, with fishing mortality corresponding to curves (p), (q), (r) and (s) of Fig. 18.17. In all but the last it follows the usual course characteristic of the simple models with constant parameters, and also—in the haddock—of models in which either recruitment or growth separately is dependent on density (but see Fig. 18.14 for plaice). With the highest value of β (curve (s)), however, quite a new feature appears; the catch per unit effort rises steeply to reach a maximum at about $F = 0.35$ and then falls, almost linearly, to reach the extinction point at $F = 1.16$. This is because growth is so slow at the high densities corresponding to low values of F that with a 70 mm. mesh the exploited phase is limited to a very few of the oldest age-groups. Although any increase in F from here must reduce the number of fish in the population

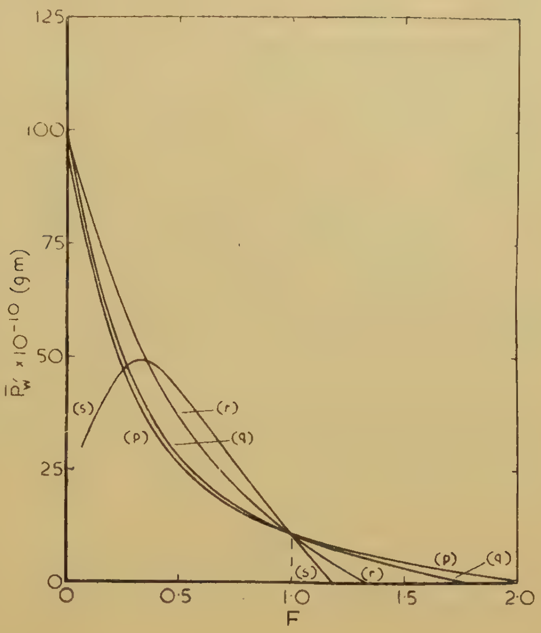


FIG. 18.19 HADDOCK: RECRUITMENT AND GROWTH DENSITY DEPENDENT

[Biomass of the exploited phase, $\bar{P}'_W$ (proportional to catch per unit effort) as a function of F with a 70 mm. mesh. Curves (p) to (s) recruitment and growth density dependent as in Figs. 18.17 and 18.18. Curve (s) is unique in that it has a maximum.]

as a whole, this reduction also accelerates growth and thus causes the span of the exploited phase to increase by allowing fish to reach the 50% selection length at an earlier age. Over the range of F between 0 and 0.3 this more than compensates for the increased mortality in the exploited phase and causes the density of the latter to increase. The conditions necessary for a maximum to appear in a catch per unit effort curve are admittedly very different from those existing in the North Sea at the present time, but not so extreme that the phenomenon need be regarded as only of academic interest, and certainly not as an artefact. For example, at a value of $F = 0.2$ on the descending limb of curve (r) of Fig. 18.19, the total biomass predicted by the model is about five to six times the mean pre-war value, with a recruitment about three times greater and an L_∞ of about 30 cm. But observed fluctuations in haddock density cover a range extending to over three times the pre-war mean (see Fig. 16.13) and the biomass of certain North Sea species such as the plaice was four to five times its pre-war level in the early part of 1946 (Margetts and Holt, 1948). Again, the recorded values of L_∞ in haddock cover a normal range of 40-70 cm., and are occasionally down to 30 cm. (see Fig. 16.13).

Since the special character of the catch per unit effort curve (s) of Fig. 18.19 is due primarily to changes in the relative abundance of the pre-exploited and exploited phases, we should not expect to find a similar maximum in the corresponding curve of total biomass. That this is so can be seen from the $\bar{P}_W$ curves of Fig. 18.20; curves (p), (q) and (r) descend throughout the range of increasing fishing mortality in the usual way, but curve (s) is flattened out at a very low value of F (< 0.1). This is similar to what was found in curve (f_2) of Fig. 18.14 for plaice; in both cases the effect on total biomass of the relatively large drop in population number that results from small increases in F from zero, is more or less counteracted by the consequent enhanced growth. It will be noticed, however, that curve (s) is not sigmoid, owing to the fall in recruitment that occurs at high fishing intensities.

We have tried in our examination of the above curves to show the way in which the population model can take some account of the interactions between reproduction, growth, and mortality—through their mutual dependence on density—that might be expected in practice, and to show how it can be used to predict their effects on yield and catch per unit effort. It will be remembered from the discussion of the relationship between egg-production and recruitment in the haddock (§15.2.3.2) that the data were too few and variable for trustworthy estimates of α and β to be obtained. To establish which of the

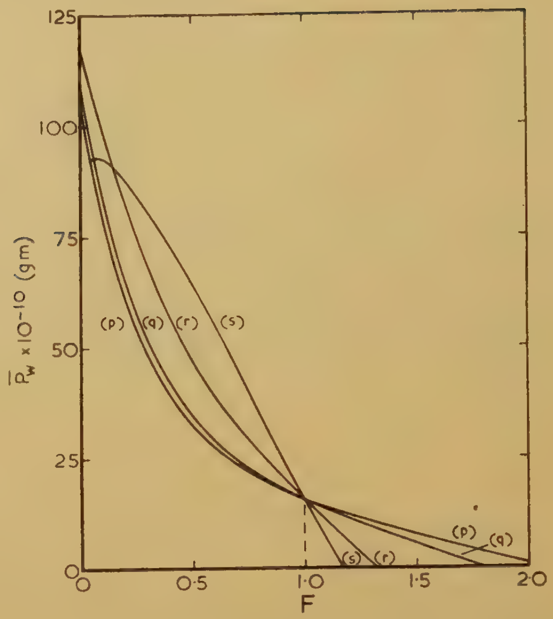


FIG. 18.20 HADDOCK: RECRUITMENT AND GROWTH DENSITY DEPENDENT

[Total biomass, $\bar{P}_W$, as a function of F with a 70 mm. mesh. Curves (p) to (s) recruitment and growth density dependent as in Figs. 18.17 to 18.19.]

curves in Figs. 18.17 and 18.18 reflects most truly the real situation, we must await accumulation of more data on egg-production and recruitment, and a better understanding of lethal processes in the larval and pre-recruit stages.

The earliest statements on conservation stressed the need for protecting the spawning stock in order to maintain the level of egg-production and hence the supply of young fish. But the virtual absence—even up to the present day—of reliable information about the relationship between egg-production and recruitment has given investigators no alternative but to assume constant recruitment—as we have done in §17—when assessments have to be made of the probable effects of changes in fishing intensity or mesh size. Because of this, there may be a danger of overstressing the importance of growth and adult mortality in determining the reaction of a fish population to exploitation, while the possible influences of sustained changes in recruitment are correspondingly neglected. The main purpose in our investigation of the properties of a theoretical model in which both growth and recruitment are density dependent has been to find—by postulating various values of α and β that are not inconsistent with such data as are available—the range of form that yield and catch per unit effort curves can exhibit, and thus to show where caution is needed when predictions based on inadequate information about recruitment have to be made.

An important conclusion is that only relatively slight changes of recruitment with abundance of spawners are needed to balance the depressive effect on the yield caused by the density dependence of growth (compare curves (b) and (p) of Fig. 18.17); to this extent the assumption of constant recruitment is a safe one because it is not likely to result in the maximum yield being overestimated—at least not much. This result might have been anticipated. What is quite unexpected is that with a rather more pronounced—though by no means excessive—degree of variation of recruitment with egg-production, the influence of density on growth might well be such that the mesh size needed to give the maximum yield for a given fishing mortality would be considerably overestimated if a constant recruitment was postulated (see Fig. 18.18, curve (r)). The opposite is true, though to a lesser degree, of the position of $(F)_{\max}$, which would be underestimated by a simple model in these circumstances. The possibility of there being a maximum catch per unit effort at a certain fishing intensity also has important implications, since the decrease in both yield *and* catch per unit effort that would result from the use of any lower intensity would certainly make the latter less profitable.

We have commented earlier in this section on the finding that with the most pronounced change of recruitment with egg-production given by the two or three highest values of β, extremely violent changes in yield are predicted by the model to result from relatively small alterations of fishing intensity or mesh size from their pre-war levels. The state of the population implied in these circumstances is indeed so precarious that it would seem to be incompatible with the behaviour of the haddock fishery during this century. This appears to set an upper limit to the value of β that can be assumed. The possibility of extinction at a value of F less than twice the pre-war value of 1.0 is present, however, with all except the smallest value of β we have investigated. But it must be remembered that the extinction values of F and mesh size given in Tables 18.12 and 18.13 refer to steady states, and in reality it would take a long time for extinction to occur even supposing that the population were continually exploited in such a way that this would eventually happen. Long before then, the declining abundance would cause the fishing intensity to slacken for economic reasons, or as Taylor (1951, p. 403) has put it . . . "it is impossible to exhaust an extensive fishery for profit because the profit disappears before the fish does". Nevertheless, questions such as these show the limitations of a deterministic theoretical model and the need for a stochastic treatment, at least of recruitment, for a proper interpretation of fluctuating data and discrimination between steady states and trends (see §§1 and 19.2.3).

18.6 VARIATION OF ANNUAL PRODUCTION WITH FISHING INTENSITY

We have so far been concerned in §18 almost entirely with the variation of yield with fishing intensity and mesh size; here we examine briefly the variation of the annual production, *A.P.*, with fishing intensity predicted by the various population models that we have set up. The *A.P.*, it will be remembered, was defined in §9.4.3.1.1 as the weight produced annually as growth by the post-recruit phase of the population, and is a characteristic having no less biological significance than the yield itself.

Equation (9.23) gives the *A.P.*, from which an expression for the annual production per recruit may be obtained by dividing both sides by R. In the first instance we may assume that all parameters are constant and take the values referring to the pre-war state of the plaice population. *A.P./R* is shown as a function of fishing mortality in curve (a) of Fig. 18.21. It falls continuously as F increases, and tends to zero as $F \rightarrow \infty$, at which point all fish are caught as soon as they enter the exploited area. In the same circumstances a similarly shaped curve is obtained for haddock.

Taking now hypothesis (b) to represent the dependence of growth on density in plaice, the variation of production per recruit with F can be calculated in this case by using

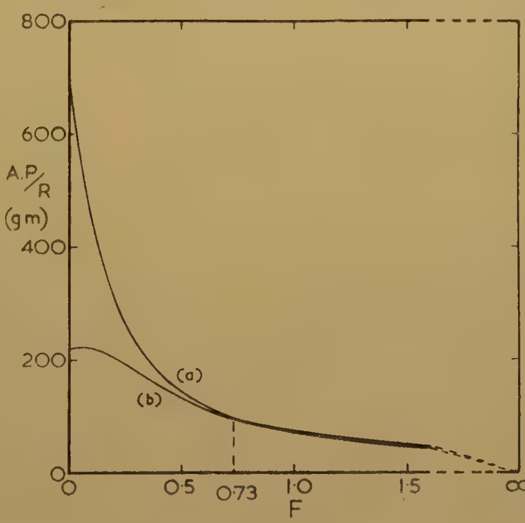


FIG. 18.21 PLAICE: ANNUAL PRODUCTION AGAINST FISHING MORTALITY

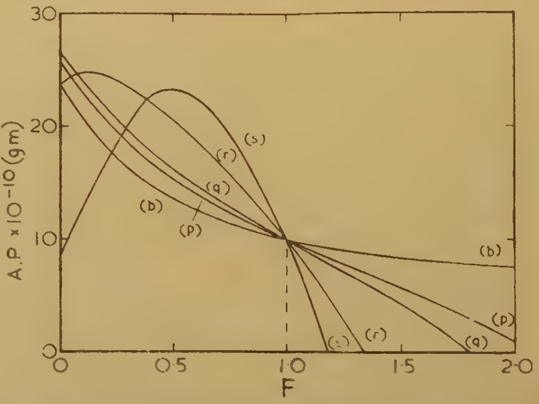
Annual production per recruit, *A.P./R*, as a function of F with a 70 mm. mesh. Curve (a) constant parameters; curve (b) density dependent growth. Curve (b) has a maximum, but this is not coincident with that of the corresponding yield curve (b) of Fig. 18.9.]

the values of W_∞ given in column B of Table 18.7, instead of the constant value of 2867 gm. This gives curve (b) of Fig. 18.21, and the marked differences between it and curve (a) at low fishing intensities will be apparent. Especially important is the presence of a maximum value of $A.P./R$ at $F \simeq 0.05$, which means that the stimulating effect on growth caused by a small amount of fishing can more than counteract the loss of individuals by capture, although the effect is only slight. There is, however, no correspondence between this maximum and that of the curve of yield for hypothesis (b), which was at a value of F between 0.3 and 0.4 (see Fig. 18.9).

Perhaps the most interesting results are those obtained when annual production is computed from the model developed in §18.5.2 in which both growth and recruitment of haddock vary with density. Using the values of R and W_∞ given in Table 18.12 for each of the four pairs of α and β, the $A.P.$ can be found directly from (9.23) giving the curves (p) to (s) shown in Fig. 18.22. Also drawn in this figure, for comparative purposes, is curve (b) for growth density dependent but recruitment constant. It will be seen that in this latter curve and those for the two lowest values of β ((p) and (q)), productivity decreases throughout the range of increasing fishing mortality, as in curve (a) of Fig. 18.21 for plaice calculated with constant parameters. With an increasing degree of variation of recruitment with egg-production a maximum appears in the $A.P.$ curve, first at very low values of F (curve (r)) and then at higher ones (curve (s)); at the same time, production in the virgin stock decreases to such an extent that the curve for the highest value of β is nearly symmetrical about the maximum.

FIG. 18.22 HADDOCK: ANNUAL PRODUCTION AGAINST FISHING MORTALITY

[Annual production, *A.P.*, as a function of *F* with a 70 mm. mesh. Curve (b) density dependent growth; curves (p) to (s) density dependent growth and recruitment. A sufficiently marked relationship between egg-production and recruitment (e.g. curve (s) can cause a pronounced maximum in the production curve.]



The differences in annual production of the virgin stock according to the particular values of α and β that are postulated seem to have some ecological significance. As β is increased so is the number of fish in the virgin stock as a result of increased recruitment; this can be seen from the values of R at $F = 0$ (which, in these circumstances, are proportional to the total number of fish in the population) for each of the curves (p) to (s) given in Table 18.11, remembering that R for curve (b) is the lowest of all since it remains constant throughout at 8.5×10^8. The intersections of the various curves with the Y-axis of Fig. 18.22 show that the $A.P.$ rises from curve (b) through (p) to (q), and falls again with (r) and (s). Thus the model predicts that in the natural state, increases in the number of fish in the population would at first increase production but that eventually a maximum productivity would be reached, beyond which reduction in growth would be so severe that it would cause the total production to fall, even though the total number of fish continued to increase. A fall in production at high densities has also been deduced by LeCren (1949) on the grounds that under such conditions less of the total food consumed is available for growth,* and also that the 'yield' obtained by the dense fish population from its food organisms may be reduced by overcropping. This last factor seems to us to be a secondary one; the main cause of a decline in production at high densities is the use of an increasing fraction of the total food consumption for maintenance at the expense of growth. Indeed, it is not unreasonable to suppose that a sufficient increase in the number of recruits would eventually reduce growth, and hence production, in the post-recruit phase virtually to zero—all the available food being used for maintenance. This is what would be predicted by our theoretical model if recruitment were increased even more, and must be what happens in practice when growth is severely retarded and adult fish stunted. The evidence for this is mentioned in §9.4.1.

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*It should be noted that LeCren's use of the phrase 'efficiency of utilisation' in this connection is not the same as ours (see §9.4.3.1.1).

It is important to remember that the foregoing conclusions relate to the post-recruit phase only; obviously the population cannot maintain, nor even perpetuate, itself without there being sufficient production for young fish to reach maturity, whether this occurs at recruitment, or at some other time. The total production must be greater than the *A.P.* as we have defined it, by at least the difference between the total weight of the recruits and the weight of the egg-batch from which they are derived, but cannot be evaluated more precisely without more knowledge of growth and mortality in the pre-recruit stages.

A subject that sometimes arises in discussion of food chains and community balance concerns the simultaneous variation in biomass, production and yield of a population according to the severity of the mortality caused in it by predators of the next highest link in the food chain (e.g. LeCren, ibid). The effect of fishing as the predatory activity on plaice and haddock can be seen by comparing the appropriate curves of §§18.4 and 18.5, from which certain general conclusions can be drawn. Thus, it is by no means inevitable that any one of the above characteristics should reach a maximum at some value of F, even if both growth and recruitment are made to vary with density. For example, curves (p) and (q) of Fig. 18.20 for $\bar{P}_W$ and Fig. 18.22 for *A.P.* in the haddock descend throughout the range of increasing fishing intensity, and the maxima of the yield curves could be removed by taking a sufficiently large mesh size (see §17.4). A maximum in a biomass curve is probably rather rare, but such curves may flatten at low values of F (e.g. curve f_2) of Fig. 18.14 and curve (s) of Fig. 18.20). Peaks in production may be more common but do not occur at the same value of F as those in the corresponding yield curves, although an approach to coincidence is found when the variation of recruitment with density is sufficiently pronounced that it is primarily responsible for the shape of both the yield and production curves (curves (s) of Figs. 18.17 and 18.22). In general, the conditions required to obtain the maximum yield are not those which result in the population being adjusted so as to have its maximum productivity, attractive though this idea may be.

18.7 Spatial Variation in the Value of the Fishing Mortality Coefficient

Of the cases discussed in §10.2 in which spatial variation in the value of parameters is important, perhaps the one of most general interest is that in which part of the exploited phase of the population cannot be fished owing to its particular location, although there is interchange of fish between it and the remainder of the population (§10.2.2). We suggested two main reasons for the existence of such a situation, namely (a) that the general exploited area includes grounds on which, because of their nature, the gear cannot be worked, but which nevertheless contain fish, and (b) that part of the area occupied by the population is permanently out of range of the fishing fleet. Since the whole of that part of the North Sea inhabited by plaice is within the working range of the fleet, the second factor is not relevant in this case. There are, however, a number of small areas that are unsuitable for trawling but which probably contain some plaice, and some adult fish are found on the nursery grounds where there is not much fishing. In addition, there are, since the 1939-45 war, extensive mine fields which, until they are cleared, make otherwise good grounds unfishable. For seines a greater proportion of the area is unfishable because this type of gear requires a smoother bottom than does a trawl. The unfishable fraction of an area is also likely to be greater for fish whose normal habitat includes rocky grounds or which may be bathypelagic for part of the time, such as hake and Arctic cod.

It is therefore probable that in nearly all major fisheries some fraction of the population will, at any moment, be protected from fishing for one or more of the above reasons, and it is necessary to obtain some appreciation of the kind of modifications to the properties of simple models that result when this factor is taken into account. There is, of course, no question of making here any precise estimate of the effect of cover in the North Sea plaice fishery, but by using figures that are of the expected order of magnitude it is possible at least to say whether the phenomenon is one that is likely to call for any drastic modifications of the conclusions reached hitherto.

The appropriate equation for investigating the effect of cover in the simplest case is (10.23), in which it will be remembered that certain parameters such as those of growth and natural mortality are taken to be the same in the fished area (A) and the unfished areas (B). The ratio of the sizes of the fished and unfished areas is denoted by z, the recruitment into each by ${}_AR'$ and ${}_BR'$ and the corresponding transport coefficients by ${}_AT$ and ${}_BT$. In the following example we suppose that the recruitment into each area is proportional to its size, that is, we can put

$$\frac{{}_AR'}{{}_BR'} = z$$

We assume also that the rate of dispersion is the same in both the fished and the unfished areas, so that ${}_AT$ differs from ${}_BT$ only by virtue of the difference in the size of the two areas, i.e.

$$\frac{{}_BT}{{}_AT} \simeq z$$

It is difficult to assess what fraction of the area occupied by North Sea plaice is unfishable, but even allowing for minefields it is unlikely to be much more than 10%, or a total area in the order of 5,000 square miles. Having in mind the magnitude of T for a statistical rectangle (one-fifth of this size) a reasonable value of ${}_BT$ for the unfished area might be about 3, with ${}_AT$ consequently having a value of $\frac{1}{3}$. In order to gain a more general conception of the effect of cover, and also to see whether the estimate of the unfishable fraction being 10% in the case of plaice is critical, we have taken a range of values of z as set out in column B of Table 18.14, although results for low values of z must be interpreted with care for reasons mentioned at the end of this section. Since we are assuming a uniform rate of dispersion, the corresponding values of ${}_AT$ and ${}_BT$ must be such that the ratio ${}_BT/{}_AT$ is equal to z, and also that their product is constant. With the particular value we have taken for ${}_BT$ when the unfishable area is 10% of the whole (i.e. 3), it happens that this constant is unity. Values of ${}_AT$ and ${}_BT$ thus defined are set out in columns C and D.

For comparative purposes it is necessary to evaluate the yield per recruit to the whole area, for which (10.23) needs to be written in the form

$$\frac{Y_W}{R} = \frac{zFW_\infty}{1+z} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{p'} - t_0)}}{\alpha_n^2 - \beta^2} \Big\{ (\alpha_n + \beta\gamma)(1 - e^{-\alpha_n\lambda} \cosh \beta\lambda) - \\ - (\alpha_n\gamma + \beta)e^{-\alpha_n\lambda} \sinh \beta\lambda \Big\} \quad .. \quad .. \quad (18.26)$$

where

$$\alpha_n = \frac{1}{2}(F + {}_AT + {}_BT) + M + nK$$

$$\beta = \sqrt{\left(\frac{F + {}_AT - {}_BT}{2}\right)^2 + {}_AT_BT}$$

$$\gamma = \frac{{}_AT + {}_BT - F}{2\beta}$$

The parameter F denotes the instantaneous coefficient of fishing mortality in the fished area, and is proportional in the usual way to the fishing intensity there.

Curves of yield per recruit plotted against F for various values of z are shown in Fig. 18.23 together with the ordinary yield curve of Fig. 17.2, which is of course that obtained when the whole of the area is fished, i.e. when $z = \infty$. It will be noted firstly that the curve obtained when 10% of the area is unfished ($z = 9$) is very similar to the ordinary yield curve and is virtually indistinguishable in the region of the maximum; while even with 25% unfished ($z = 3$) the differences are not great. Therefore it seems reasonable to conclude that the fact that a small part of the plaice area is unfishable does not necessitate any modification of our previous assessments. On the other hand, when a large fraction (e.g. 50% or more) of the area is unfished profound changes in the shape of the yield curves appear; in particular, the value of $(F)_{\text{max}}$ increases until, when the fished area is only 10% of the whole ($z = 0.111$), it is no longer within the range that we have investigated. This curve could be taken to represent the kind of yield curve to be expected in a primitive or fringe coastal fishery in which boats cannot go far from port, i.e. in which the 'availability' is low (see §10.2.3).

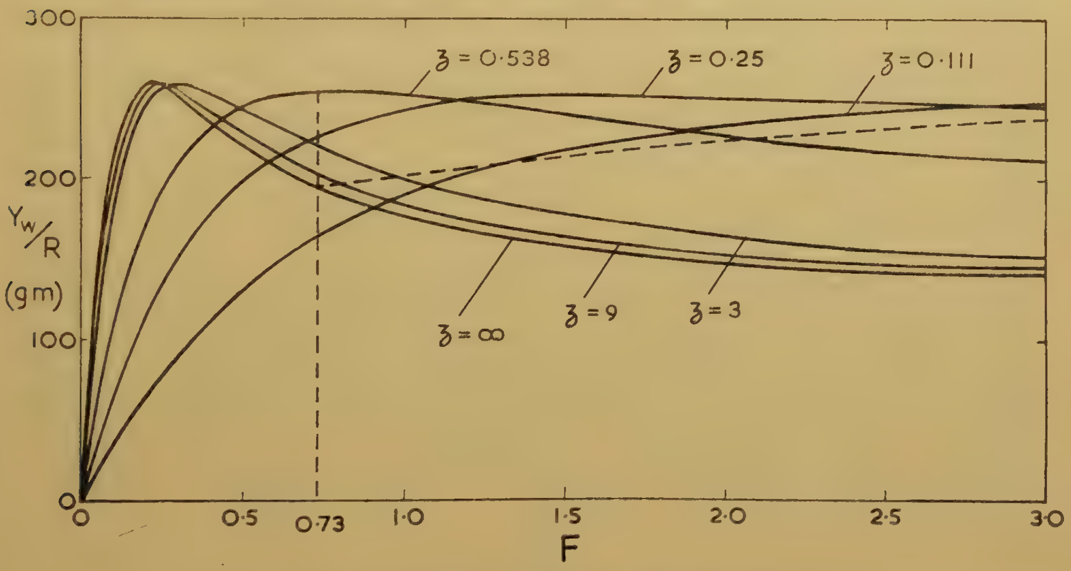

FIG. 18.23 PLAICE: FISHING RESTRICTED TO VARYING FRACTIONS OF THE AREA INHABITED BY FISH

[Yield per recruit, Y_W/R, as a function of F (the fishing mortality coefficient in the fished area) with $t_{\rho'} = 3.72$ yrs. Each curve refers to a different ratio of fished to unfished areas, these being defined by the value of z (see Table 18.14, p. 000). The broken curve shows the effect on yield of restricting a constant fishing effort (i.e. that which would generate a value of $F = 0.73$ if the whole area were fished) to a progressively smaller fraction of the whole area.]

The yield curves of Fig. 18.23 can also be used to gain some idea of the effect of closing certain areas to fishing as a regulative measure. A rather different interpretation is required for this, since the effect of prohibiting fishing in part of the area would usually be to concentrate the same total effort in the remainder. If it is supposed that a constant fishing effort is initially distributed over the whole area and generates a mortality F_∞, then the value of F_z corresponding to any particular value of z resulting from closure is

$$F_z = \frac{F_\infty(1 + z)}{z}$$

The broken curve of Fig. 18.23 shows the effect on the yield of increasing the fraction of the whole area that is closed to fishing, assuming the constant total effort to be that which, when distributed over the whole area, generated the pre-war value of $F = 0.73$. The curve therefore starts at this value of F on the yield curve for $z \rightarrow \infty$ and it is seen that increasing the size of the closed area causes the yield gradually to increase within the range investigated. It therefore appears that closure would have some beneficial effect, but that a large fraction of the whole area would have to be closed to produce any marked increase in yield. It is in these circumstances, however, that the simplified representation of dispersion by means of transport coefficients is least satisfactory, which is a matter we must now consider.

In §10.2.2 it was shown that the model formulated by (10.23) from which (18.26) is derived gives a reasonably good representation of the case in which the unfished part of the whole area consists of a number of smaller areas. Thus it is applicable to an analysis of the effect of cover when the latter consists of isolated areas unsuitable for trawling that together are only a small fraction of the whole area, as in the plaice fishery. It is least satisfactory when the fished area is small relative to the unfished area (i.e. at low values of z), as would be the case if a large part of the whole area were closed to fishing as a regulative measure. In these circumstances a high fishing intensity would cause a marked density gradient into the unfished area from its boundary with the fished area, the density just inside the unfished area being less than its average density. Hence transport into the fished area would be less than is predicted by (18.26), in which it is assumed to proceed at a rate proportional to the average density. As a result, the true yield curves for low values of z would be rather lower than those shown in Fig. 18.23, especially at high values of F, and the dotted curve showing the effect of closure with the effort constant would not increase with F to the same extent. Indeed, the regulative benefit of closure must be regarded in general as problematical, and certainly could not be assessed without a detailed knowledge of fish movements in relation to the particular areas it is proposed to close.

The calculations described above are based on one rate of dispersion only, which is assumed uniform over the whole area, but it is possible to see the kind of effects that would result in certain other conditions. Thus more rapid dispersion would mean that decreasing z would have less effect on yield curves than in Fig. 18.23; while if dispersion were slow enough, decreasing z would amount in effect to reducing recruitment to the fishable part of the population, since replenishment from the unfished areas would be negligible. Qualitatively similar differences would be found if dispersion in the unfished area was more or less rapid, respectively, than in the fished area.

18.8 Conclusions from §§17 and 18, and their Relevance to the Past History of the North Sea Plaice and Haddock Fisheries

The conclusions reached from a study of the simple models of Part I applied to plaice have been summarised in §17.6. The main one is that a rather greater sustained yield could apparently have been obtained during the pre-war years with either a substantially lower fishing intensity or a larger mesh than was then employed. Essentially the same is true for haddock (§17.7), although the potential increases in yield to be obtained by changes of these kinds do not seem to be as great.

The outstanding impression from the investigations in the present section of the properties of more complex population models is that these conclusions still hold good, though they need to be modified in degree. Some of the complications are found to have very little effect on the shape of yield curves; examples are the accurate representation of the selection ogive (§18.1) and the variation of weight among fish of the same age with its effect, when combined with a weight-threshold, of causing recruitment to occur in several age-groups (§18.3.1). Other phenomena, notably the density dependence of growth (§18.4) and natural mortality (§18.2), have more significant effects, and certainly cannot be neglected when predicting the result of a proposed change in fishing intensity or mesh size (especially the latter), though the amount of change of growth with density that has been detected in the plaice and haddock is not, in itself, sufficient to invalidate the earlier conclusions. Very little is known about the density dependence of natural mortality, but in plaice at least there is evidence that it is not critical. Finally, there are two factors which could potentially cause certain conclusions drawn from simple models to be entirely fallacious. These are the variation of recruitment with density (combined with that of growth, §18.5.2) and the restriction of fishing to part only of the area inhabited by the fish population (§18.7). The latter does not apply to any great extent in either the plaice or haddock fisheries, but a large increase in abundance above the pre-war level would probably cause some change in the average recruitment, even though it might not be possible to establish it conclusively until data for a number of years were available. Such evidence as is available for plaice points to recruitment being near to an asymptotic level, with egg-productions of the magnitude that occurred in pre-war years. In this species, taking recruitment to be constant when investigating the probable effects of decreasing the fishing intensity or increasing the size of mesh is, therefore, reasonable as a working assumption. In haddock, on the other hand, the increases in population abundance that would be caused by such changes may result in a noticeable increase in recruitment, with consequences of the kind discussed in §18.5.2.

The modifications of the earlier conclusions that are necessary can be summarised as follows. A maximum in the yield-fishing intensity curve, with the pre-war mesh in use, probably occurs at a fishing intensity rather higher than that predicted from the simple models: at between a third and a half of the pre-war intensity in plaice, and at very roughly a half of it in haddock. Also, the maximum of the yield-mesh curve at the pre-war fishing intensity occurs at a smaller mesh than predicted from the simple models, but probably at not less than about 150 mm. in plaice and 95-100 mm. in haddock. It is more difficult to predict the magnitudes of these maximum yields because they depend critically on the extent to which recruitment would increase with a spawning population several times more abundant than during the pre-war period. Having in mind the relatively small increase in recruitment that is needed to counteract the lowering of the maxima caused by the density dependence of growth, it seems reasonable to conclude that the true maxima are not lower than those predicted by the simple model and are probably higher, especially in haddock.

The properties of the various theoretical models form a consistent pattern that has obvious implications concerning the exploitation of the plaice and haddock stocks and that provides a satisfactory explanation of the trends in them since the beginning of the century. During this time these fisheries had no effective regulation, and statistics provide a practical demonstration of the unrestricted development of a commercial fishery that agrees closely with what would be predicted from the theoretical model. The evidence has been fully documented and analysed elsewhere, especially in the publications of the International Council for the Exploration of the Sea*, and here we need do no more than remind the reader of the main features. These are that after increasing during the first part of the period, the total fishing intensity tended to become stable during the later years between the two world-wars, and a rough balance was set up between the amount of fishing on the one hand and the natural productivity of the stocks on the other. Yet all the indications are that the balance reached was not the one most favourable to man; the yield of plaice and some other species was no more than before the first world-war, and that of haddock was appreciably less, despite the fact that the fishing intensity was, as far as can be judged, between one and a half times and twice as high in the later period as in the earlier. The indications are, in fact, that the few years immediately before the first world-war saw the nearest approach to the conditions required for obtaining the maximum steady yield with a mesh of 70 mm. or less. The fact that the fishing intensity was then nearly half that during the nineteen thirties is in accordance with the conclusions from the properties of theoretical models, summarised above. The consequence of continued increase in fishing beyond that needed to produce the maximum sustained yield was that the fishing industries of many countries were forced to operate at an undesirably low economic level, and the resulting lack of incentive to increase the size of fishing fleets brought about the stability

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*Particularly relevant are the papers presented at the Special Meeting of the Council in 1939, which are published in *Rapports et Procès-Verb.*, vol. 110, 1939.

referred to above.* It is significant that these trends in the North Sea demersal fisheries had parallels in the Pacific halibut fishery before regulation was introduced.†

We do not propose to attempt here a more detailed interpretation of early data; something more may indeed be possible but the virtual absence of reliable data on fishing intensity and age-composition is a serious limitation, as has been stressed by Graham (1951a). It is worth noting, however, that in addition to the broad agreement between the actual changes in yield and effort and those predicted from theoretical models, there is abundant evidence (e.g. Thursby-Pelham, 1939, for plaice) that as fishing intensified the decrease in average age and weight of fish in the catch that would have been expected from theory did occur in practice. Huntsman in 1951 was perhaps formally correct in claiming that it had yet to be demonstrated that it is beneficial to let fish grow older before being caught; but only the Pacific halibut fishery had then been regulated (by reduction of fishing effort‡) and in this instance the kind of data needed to demonstrate this effect conclusively have not been published. We suggest that the changes accompanying the increase of effort in the North Sea plaice and haddock fisheries at least establish the converse with some certainty, while the effects of the cessation of fishing during both the world-wars are clear proof that the downward trends in productivity and economic condition are reversible.

If experience alone—even without confirmation from theory—is seemingly so unambiguous in its demonstration of excessive depletion in the North Sea demersal fisheries, it might be thought that the fishing industries would themselves have taken before now the steps necessary to remedy the situation. The main reason why this has not happened, and can scarcely be expected to happen in the future, is of course the basic competitive element in fishing. Thus the initial effect of a reduction in fishing effort is, inevitably, some loss of yield (see §19.2.2.1); while reduction of effort by one section of an industry, or by the industry of one country alone among several working in the same area, may bring no benefits to that section even after the transitional period (see §19.3). Hence we are led to the inescapable conclusion that some form of external regulation is essential to obtain the best results from the exploitation of a fish stock, and even, in many cases, to prevent the natural tendencies for expansion of fishing effort and improvement in fishing methods from seriously reducing the productivity of the fishery and the economic state of the industries concerned. We now turn to the problem of establishing the principles on which regulation should be based, and a discussion of some of the factors that need to be taken into account when actual regulative proposals are framed.

SECTION 19: PRINCIPLES AND METHODS OF FISHERY REGULATION

The state of the North Sea plaice and haddock fisheries during the nineteen thirties, summarised in §18.8, can be described as one of 'overfishing', using this word in the general sense adopted by Graham (1951a) to mean simply 'too much fishing'. One possible form of regulation therefore seems self-evident, namely to reduce the fishing mortality coefficient in the population by decreasing the fishing intensity. On the other hand, we have shown that increasing the size of mesh could also improve the state of these fisheries;

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*Since equilibrium in an unrestricted fishery results when a minimum profit level is reached, differences in the economic backgrounds of the fishing industries of the various countries fishing the North Sea would prevent an equilibrium of this kind being attained simultaneously in each. In fact, statistics show that the British fishing effort was one of the first to reach the limit of its expansion and even began to recede slightly in 1937 and 1938 (see App. III); Danish fishing effort, on the other hand, was still increasing fairly rapidly at this time.

†See, e.g., *Introduction to Rep. Int. Fish. Comm. No.* 16, 1951.

‡Reduction of fishing effort was the indirect effect of regulation by catch limits (§19.2.1.1).

in fact, we concluded in §17.6 that to obtain the best yields from the plaice, changes in both fishing intensity and mesh size would be necessary, and none of our findings in §18 has shown this to be false.

Our first task is therefore to establish a rational basis on which changes in these two characteristics of fishing activity can be made so that they may be most effective. This defines the form of regulation that is required. There is then the question of specifying the ultimate objective of fishery regulation, or, in other words, of deciding not only the direction in which changes in fishing intensity or mesh size or both should be made in any particular case, but also how far they should be taken to produce the best results. The factors entering into such a decision are numerous, and include economic and social criteria, as well as biological. Some of what has been written previously on this subject will be reviewed in §19.1.6; in venturing to discuss it further ourselves we are not unmindful of the fact that we can offer no special knowledge of economic theory. Our main purpose is to clarify the parts played by biological and economic factors in determining the requirements for the ideal level of exploitation, which is neither overfishing nor underfishing, and which we call optimum fishing.*

All this is the subject of §19.1. In addition to the question of the fundamental objectives that fishery regulation is designed to achieve, a number of practical questions arise when actual regulative methods come to be framed and put into operation. These include the choice of regulative method (§19.2.1) and the events during the transitional phase between the introduction of regulation and the attainment of the new steady state (§19.2.2); while in §19.2.3 we discuss briefly problems conveniently grouped under the heading of fishery maintenance, such as that of testing whether regulation has had the desired effect and of detecting any change in the dynamics of the fish population that would call for a revision of the regulative measures. Finally, in §19.3, we analyse the special features of an international fishery—of which the North Sea demersal fisheries are of course examples—and some of the problems involved in regulating it.

Some of the questions that we cannot avoid mentioning in this section are more matters of administration and policy than purely scientific problems, but all must be assessed ultimately against the background of the dynamics of the fish populations. Our purpose here is primarily to show how the theoretical models whose properties have been investigated in §§17 and 18 can be used to define more clearly the objectives of fishery regulation and to guide administrative action. In so doing we aim to provide a basis on which, in §20, specific regulative proposals for the North Sea can be formulated.

19.1 The Concepts of Eumetric and Optimum Fishing

19.1.1 *Eumetric yield and fishing curves*

A characteristic of many of the curves showing changes in yield with fishing mortality, which we have presented in §§17 and 18, is the existence of a maximum value of yield within the range of fishing mortality that has been observed. The first point to note is that these maxima occur in curves obtained from models in which the number of annual recruits is constant, so that they are the result only of the interaction of fishing mortality, natural mortality and growth. Evidently, then, we do not need to postulate the dependence of numbers of recruits on population density in order to obtain a maximum yield although, when this is done, the maxima are made sharper and the possibility of extinction arises at high fishing intensities (see §18.5.2).Our models therefore offer a means of distinguishing between the two factors that have long been recognised as being decisive in problems of exploitation, namely, the importance of allowing fish to grow to a reasonable size before catching them, and leaving enough fish in the sea to spawn and keep up the stock level (see Graham, 1948, p. 47).

Now, if it should be a *general* feature of the reaction of a fish population to exploitation that a maximum value of yield occurs at a certain fishing mortality, this would have an immediate bearing on the problem of defining the best level of exploitation. Our analysis has shown that this is not so. Thus, a much increased value of the natural mortality coefficient can completely remove the maxima which have been found in curves of yield as a function of fishing mortality in both plaice and haddock (see Fig. 17.18.1 for plaice). Moreover, to make $(F)_{\max}$ greater than about 1·5, which corresponds to the limit of the range of fishing intensity that we need consider, the values of the natural mortality coefficient required are not greater than might occur if these fish populations were intensively grazed by a predatory species. The particular form and intensity of certain density dependent relationships—notably those of growth and natural mortality, also have a bearing on the existence of such maxima, as shown in Figs. 18.3 and 18.9.

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*Since this was written, notable advances have been made in the economic theory of fishery resource utilisation, in particular by Scott Gordon (1953, 1954) and Gerhardsen (1952).

More important, however, is that the existence of a maximum in a curve of yield as a function of fishing mortality depends on the age, $t_{\rho'}$, at which fish enter the exploited phase, and hence, in effect, on the selective properties of the gear in use. This is shown by the isopleth diagrams of yield per recruit (Figs. 17.14 and 17.26), in which the dotted lines AA′ give the value of $(F)_{\max}$ for any value of $t_{\rho'}$. These lines, for both species, ascend to an asymptote at a continually decreasing rate, so that above a certain value of $t_{\rho'}$, $(F)_{\max}$ lies outside the working range and eventually becomes infinitely great as $t_{\rho'}$ increases further. A more direct way of showing this is to plot curves of Y_W/R against F for various values of $t_{\rho'}$, as in Fig. 19.1. As we anticipated, we must therefore consider changes in both fishing intensity and gear selectivity to arrive at a generalized concept of rational exploitation.

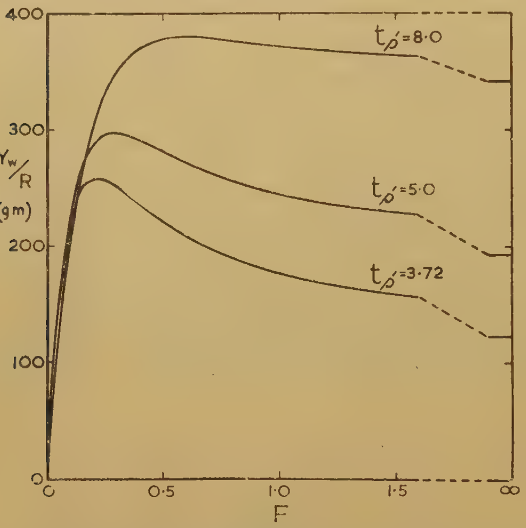

FIG. 19.1 PLAICE: EFFECT OF DIFFERENT GEAR SELECTIVITIES ON SHAPE OF YIELD—FISHING MORTALITY CURVES

[Yield per recruit, Y_W/R, as a function of F for various values of $t_{\rho'}$. As $t_{\rho'}$ is increased the height of the maxima of the yield curves is at first raised and $(F)_{\max}$ increased, but the maxima become progressively less marked and eventually disappear.]

To develop the argument further, we now suppose that we are dealing with a commercial fishery in which a single major species is being exploited by one fleet, all vessels of which are using gear with the same selective properties, i.e. that generates the same value of $t_{\rho'}$. Further, we suppose that we are free to adjust the total fishing intensity and the selective properties of the gear over as wide a range as may be required, and that the yield-isopleth diagram for the species conforms to the general type illustrated in Figs. 17.14 and 17.26. This is, admittedly, a particularly simple case, but no essential feature of actual fisheries is absent from it; some of the complications that exist in practice are discussed in §19.1.5, but they do not invalidate the conclusions drawn here. Without anticipating the question of how or on what basis a fishery should be regulated, we take it as axiomatic that a prime motive in any *commercial* fishery is to obtain as much income, in the form of yield, as is possible with a given expenditure in fishing. Thus the basic variables are now not yield and fishing intensity but their economic equivalents of value and cost. However, this transformation is a complex process and to treat it in detail at this stage would detract from the main theme we wish to develop. For the moment, therefore, we continue with yield and fishing intensity as the main variables, it being sufficient at this stage to assume that the magnitude of the annual yield and its value, and also that of the fishing intensity and the cost of generating it, would at least increase or decrease together within the range considered, even if they are not proportionately related.

It will be remembered from the discussion of §17.4 that the line BB′ of the yield-isopleth diagram defines, for a given fishing intensity, the value of $t_{p'}$ (and hence the gear selectivity) that must be used to produce the greatest yield with that particular intensity. Now the cost of using a highly selective gear (e.g. a large mesh) is unlikely to differ appreciably from that of a gear of low selectivity (e.g. a small mesh); this is certainly true of trawls and seines within the range of mesh size that need normally be considered (see §19.1.5.1). Therefore it follows that adjusting the characteristics of the fishing activity so that it generates a pair of values of F and $t_{p'}$ lying on the curve BB′ enables the greatest yield to be obtained for a given cost of fishing, and therefore satisfies the basic requirement of commercial fishing.* Such pairs of values of F and $t_{p'}$, together with the combinations of fishing intensity and gear selectivity needed to generate them, we shall term *eumetric*,† and the line BB′ itself the *eumetric fishing curve.*

The yield at each point on a eumetric fishing curve can be deduced from the contours of an isopleth diagram, but the variation of yield along it can be shown more clearly by plotting directly the curve of yield as a function of eumetric fishing intensity, that is, with the gear selectivity varying throughout in such a way that all values of F are associated with the corresponding values of $t_{p'}$ defined by the line BB′. Such curves are shown for plaice and haddock by the full lines P(a) and H(a) of Figs. 19.2, using the simple models of Part I, and we refer to them as *eumetric yield curves.* They could be constructed directly from the isopleth diagrams of Figs. 17.14 and 17.26, though it is better to read off $(Y_W/R)_{\max}$ at $(t_{p'})_{\max}$ from curves of Y_W/R against $t_{p'}$ for selected values of F. It is important to note that the value of F associated with any value of $t_{p'}$ according to the line BB′ of Figs. 17.14

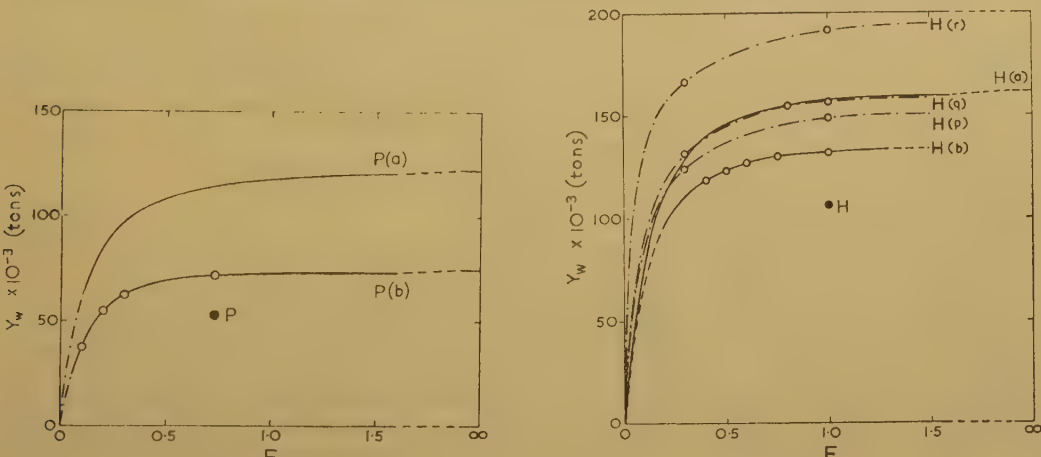

Fig. 19.2.1

Fig. 19.2.2.

FIGS. 19.2 PLAICE AND HADDOCK: EUMETRIC YIELD CURVES

[With eumetric fishing the selectivity of the gear is adjusted so that the maximum yield is obtained with each intensity of fishing. This relationship, in terms of F and $t_{p'}$, is defined by the line BB′ of the yield-isopleths of Figs. 17.14 and 17.26. These diagrams show yield as a function of F with $t_{p'}$ (or mesh) varied in this way, and are called eumetric yield curves.]

Fig. 19.2.1 Plaice: curve P(a) constant parameters; curve P(b) growth density dependent. The point P shows the mean pre-war European yield of North Sea plaice.

Fig. 19.2.2 Haddock: curve H(a) constant parameters; curve H(b) growth density dependent; curve H (p), (q) and (r) recruitment and growth density dependent as in Figs. 18.17 and 18.18. The point H shows the mean pre-war European yield of North Sea haddock.

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*It will be seen that the line AA′ does not satisfy this requirement, since for any value of F a greater yield could be obtained at no greater cost by increasing the value of $t_{p'}$ until the line BB′ is reached.

†This term has been suggested to us by Mr. John Graham, and is derived from the Greek ευμετροσ—well-proportioned (Beverton 1953). Allen (1953) has shown, in effect, that with eumetric fishing, the ratio of the weight of fish at first capture to the average weight of fish in the catch is equal to $F/F+M$.

and 17.26 is *below* $(F)_{\max}$ of the corresponding curve of Y_W/R as a function of F for that value of $t_{p'}$, and so also is Y_W/R below $(Y_W/R)_{\max}$. In plaice the eumetric values of $t_{p'}$ at values of F less than about 0·1 are lower than the age at recruitment, t_p; hence between $F = 0$ and $F = 0{\cdot}1$ it is necessary to keep $t_{p'}$ constant at 3·72 years, and the curve is therefore drawn broken in this region (see §19.1.5.2 for a fuller discussion). The curves of Figs. 19.2 have been plotted in absolute units of yield for reasons that will appear shortly; for the moment this has no effect on our conclusions, since we have only multiplied the yield per recruit values by the pre-war mean annual recruitment in each species.

The most important feature of the eumetric yield curves P(a) and H(a) of Figs. 19.2 is that they have no maximum but ascend continuously to an asymptotic value of yield as $F \rightarrow \infty$. In models with constant parameters this yield is the greatest total weight attained by a year-class during the course of its life—actually, at an age given by the corresponding value of $t_{p'}$. It is, in fact, what Herrington (1943), Nesbit (1943) and Ricker (1945) have termed the 'optimum catch', since it is that which would be obtained by allowing a year-class to reach its greatest total weight and then catching all of it at once. It is important to note, however, that this interpretation of the asymptote of a eumetric yield curve and definition of the maximum possible catch obtainable from a stock are valid only when factors are independent of population density. We discuss this point further below, but it raises the question of whether the shape of the eumetric yield curves P(a) and H(a) has any general significance in view of the fact that they are calculated from simple models with constant parameters; in particular, of whether the absence of a maximum can be regarded as a fundamental property of such curves.

This is not a question to which we can give a categoric answer, but at least we can say that none of our investigations so far have given a eumetric yield curve for a single species that has a maximum; there are, moreover, other reasons for believing that this result is sound as a working generalisation. The values that are assigned to parameters simply decide the particular age at which a year-class reaches its greatest total weight. For example, using parameter values other than those of §17 alters the general level of the eumetric yield curves and causes them to ascend to different asymptotes. Thus a larger natural mortality or a slower growth would result in a lower asymptote, and vice-versa.

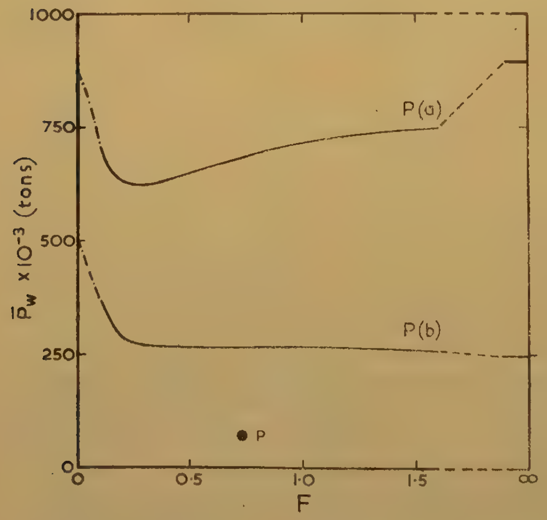

FIG. 19.3 PLAICE:
TOTAL BIOMASS AGAINST FISHING MORTALITY WITH EUMETRIC FISHING

[Total biomass of post-recruit phase, $\bar{P}_W$, as a function of F with eumetric fishing. Curve P(a) constant parameters; curve P(b) growth density dependent; these correspond to curves P(a) and P(b) of Fig. 19.2.1. The point P shows the mean pre-war biomass of plaice. Note that with eumetric fishing, biomass remains nearly constant over a wide range of F, especially when a density dependent growth is incorporated.]

More difficult is to anticipate the effect caused by introducing density-dependence. In this case the greatest weight attained by a year-class, and the age at which it is reached in the absence of fishing, would not remain the same when fishing started because of the change in density that this would inevitably cause. However, the eumetric combinations of F and $t_{p'}$ specified by the line BB′ of the yield-isopleth diagram are such that there is a tendency for the total biomass of the post-recruit phase, $\bar{P}_W$, to be maintained at roughly the same level throughout, because increasing $t_{\rho'}$ tends to increase the total biomass, while increasing F tends to reduce it. Curve P(a) of Fig. 19.3 shows the biomass, $\bar{P}_W$, as a function of F corresponding to the eumetric yield curve P(a) of Fig. 19.2, and it is seen that compared with the curves with the mesh held constant (e.g. Fig. 17.3) the change of biomass involved is small. As a consequence, dependence of parameters on population density would not be expected to have much effect on the shape of a eumetric yield curve, simply because no great change in density is involved. On the other hand, *all* eumetric combinations of F and $t_{\rho'}$ in plaice and haddock give rise to biomasses that are considerably greater than were found for these species under pre-war conditions (see point P of Figs. 17.16 and 19.3); hence we should expect the introduction of the density dependence of factors such as growth to tend to lower all points on the curves of eumetric yield and biomass calculated with constant parameters, whereas that of recruitment would be expected to raise the whole level of the curve. The effect on the biomass curve of the density dependence of growth in plaice is shown by curve P(b) of Fig. 19.3; it will be seen that not only is it much lower than curve P(a) but is even more nearly horizontal. Only at very small values of F is any appreciable change in biomass involved, and this is due partly to the fact explained above that eumetric values of $t_{\rho'}$ cannot be attained for values of F below about 0·1 in plaice.

The calculation of complete isopleth diagrams of yield with parameters density dependent is extremely laborious; but it is possible to compute the eumetric yield curve itself in a shorter way by selecting a few values of F and constructing enough of the yield-mesh curve for each value of F to estimate the maximum yield (and, incidentally, the mesh size to which it corresponds, as will be seen below). The eumetric yield curve for plaice found in this way using hypothesis (b) to represent the density dependence of growth is shown by curve P(b) of Fig. 19.2.1. The known points on this curve are indicated by circles, that at $F = 0{\cdot}73$ being the maximum value of yield in the yield-mesh curve of Fig. 18.11 converted to absolute units by multiplying by the mean pre-war value of $R = 2{\cdot}8 \times 10^8$ (see §15.2.1). It will be noted particularly that among the known points is that for the yield at $F = \infty$. We have not established conclusively that the curve does not reach a maximum between $F = 0{\cdot}73$ and ∞, but from the shape of the known part of the curve this seems unlikely; certainly, if a maximum does exist, it must be at a value of F well outside the range we need consider.

The eumetric yield curve for haddock with growth density dependent (using the relationship deduced in §16.4.1.2) is shown by curve H(b) of Fig. 19.2.2, in which the known points are indicated by circles as before. In this case we have not computed the value at $F = \infty$, but there is no reason to believe that the curve is other than asymptotic. We have also computed a few points on the eumetric yield curves for haddock using the theoretical model investigated in §18.5.2 in which both growth and recruitment are density dependent. These are curves H(p), H(q) and H(r) of Fig. 19.2.2, the lettering being the same as that adopted in §§15.2.3.2 and 18.5.2 and referring to the three lowest values of β given on p. 273. Admittedly, the precise shape of these curves is not known but the position of the calculated three points on curve H(q) virtually rules out the possibility of a maximum within the range investigated. It is interesting to find that the degree of variation of recruitment with egg-production specified by the second pair of values of α and β (see curve (q) of Fig. 15.15) happens to counteract almost exactly the depression caused by the density dependence of growth alone, and results in a curve that is remarkably similar to H(a) calculated with constant parameters. This result is of special interest because obtaining the maximum possible yield from a stock when recruitment is density dependent is not merely a question of catching all fish of a year-class when the latter reaches its greatest total weight; equally important, and possibly in some cases more so, is the need to fish the population in such a way that egg-production is sufficient to maintain recruitment at the best level—this, specifically, not being necessarily the maximum possible recruitment. These two criteria, which have long been recognised as the key factors in fishery conservation, are incorporated in the eumetric yield curves H(p), (q) and (r) of Fig. 19.2.2.

The eumetric fishing curves (i.e. those defining the eumetric relation between fishing intensity and gear selectivity) corresponding to the eumetric yield curves of Figs. 19.2 are shown in Figs. 19.4 with the same lettering. Again it will be seen that the introduction of density dependence involves no fundamental change in shape, but in every case the curve is lower than that predicted with constant parameters, i.e. a smaller mesh than before is eumetric with any given value of F. This is partly because all the more complex models we have used incorporate the density dependence of growth, and since the density at any point on the eumetric curves is greater than in the pre-war state, growth is slower and a smaller mesh size is needed to produce a given value of $t_{p'}$. Thus whereas the effect of increasing the change of recruitment with egg-production is to increase the eumetric yield at all values of F, the eumetric mesh size becomes progressively smaller because growth is correspondingly slower (cf. curves H(p), (q) and (r) in Figs. 19.2.2 and 19.4.2). It can be expected that the same thing would happen with a density dependent natural mortality rate, even if growth were constant; in this case the maximum total weight would be attained by a year-class at a lower value of $t_{p'}$, so that the eumetric mesh size would also be lower than if the natural mortality had been constant.

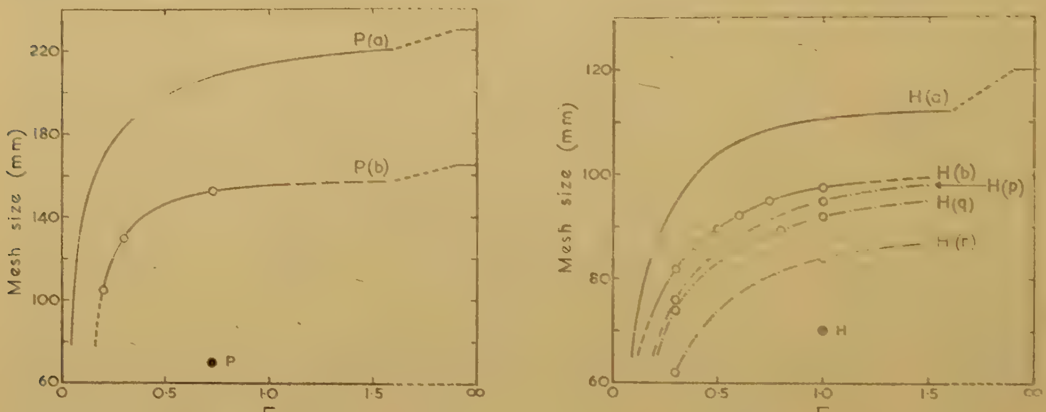

Fig. 19.4.1 Fig. 19.4.2

FIGS. 19.4 PLAICE AND HADDOCK: EUMETRIC FISHING CURVES

[These define the relationships between F and mesh size involved in the eumetric yield curves of Figs. 19.2.]

Fig. 19.4.1 Plaice: curve P(a) constant parameters; curve P(b) growth density dependent. The point P shows the pre-war conditions of $F = 0{\cdot}73$, mesh = 70 mm.

Fig. 19.4.2 Haddock: curve H(a) constant parameters; curve H(b) growth density dependent; curves H(p), (q) and (r) recruitment and growth density dependent as in Figs. 18.17 and 18.18. The point H shows the pre-war conditions of $F = 1{\cdot}0$, mesh = 70 mm.

To summarise, we suggest that the concept of eumetric fishing provides a rational basis for the mutual adjustment of the two biological characteristics of fishing activity that can be varied by regulation, namely the fishing mortality coefficient F and the age of fish $t_{p'}$ at which that mortality first becomes effective. It leads to the eumetric yield curve as the generalised yield-intensity curve of a fishery, in which the value of $t_{p'}$ is not constant but is varied by changing the selectivity of the gear in such a way that it is eumetric with any value of F. For a single species, everything points to the conclusion that such yield curves have no maximum—not, at least, within the working range of F—but as $F \to \infty$, tend asymptotically towards a limit which is the greatest possible yield obtainable from the population.

19.1.2 *The objective of optimum fishing in general terms*

We turn now to the second part of the problem of defining in general terms the objectives of fishery regulation. From the foregoing it follows that this amounts to an analysis of the factors relevant to deciding at which point on a eumetric yield curve it would be best for the fishery to operate or, in other words, which eumetric combination of fishing intensity and mesh size it would be best to use.

It is now possible to see the significance of the conclusion reached above that a eumetric yield curve for a single species almost certainly has no maximum at any finite value of F. It means that there is no biological criterion that can be used as a guide to where it would be best for a fishery to operate. Thus the maximum possible yield, i.e. the asymptote of the eumetric yield curve, can be attained only with an infinitely high fishing intensity and hence at a correspondingly high cost; it is therefore a totally unreal objective for regulation—not for any biological reason but on purely economic grounds. It seems that some sacrifice of yield must be made in order to reduce the cost of fishing to a level at which it is a reasonably profitable undertaking, and it is partly in terms of factors such as these—factors that we refer to, broadly, as economic and social—that the objectives of fishery regulation must be framed.

Essentially the same argument has been put forward by Huntsman (1951), who points out that. . . . "the highest take is not necessarily the best", and, again, that "It is a continuing economic problem to ensure sufficiently high take per unit of effort for profitable fishing". Huntsman has in mind the case in which it is a practicable possibility to obtain a maximum yield, yet in the same circumstances Burkenroad (1953) has suggested that it would be difficult to find any "tangible nett gain" from reducing fishing intensity below that giving the maximum steady yield. With eumetric fishing, however, it is quite impossible to avoid this issue since the whole of the eumetric yield curve is comparable, in effect, with that part of an ordinary yield curve that lies to the left of the maximum. Earlier, the importance of the economic conditions under which the yield is obtained had been stressed by Graham (1935, p. 264, see also 1952 for fuller review) in saying that. . . . "the benefit of efficient exploitation lies more in economy of effort than in increase of yield, or preservation of future stocks, though both of these purposes may also be served".

This same dichotomy of regulative function has been discussed in detail by Herrington (1943) and Nesbit (1943), who use the terms 'conservation' to mean regulation designed purely to increase the yield, and 'economic management' for regulation that is concerned with the economic and social conditions in the fishing industry, i.e. the conditions under which the yield is obtained. Herrington regards these as independent objectives for regulation, with economic management to be undertaken or not according to policy; while an exactly similar position is adopted by Foerster (1950, p. 10) in stating that "Any considerations beyond those of conservation may or may not, depending on one's viewpoint, be the function of fisheries regulation". Nesbit, on the other hand, while agreeing with Herrington in regarding conservation as the primary objective, believes that both should always be considered. Now both Herrington and Nesbit were supposing that a fishery can provide a maximum catch and that this is a practicable objective for regulation. We have shown above that with eumetric fishing this is not so, but there is, nevertheless, a greatest yield that it is economically possible to obtain, and it is instructive to consider for a moment what would happen if it were taken as the objective of regulation. For this strictly conservative purpose, regulation would be limited to ensuring that the selective properties of the gear were always eumetric with whatever fishing intensity was being exerted. The latter would not be regulated, and economic incentive would cause it to increase until a point on the eumetric yield curve was reached at which the profit margin was so low that the incentive no longer existed. This steady state would differ from that reached in the absence of regulation of any kind (e.g. as in the North Sea between the wars, see §18.8) only in that the yield would be rather larger because the mesh size would be eumetric—it would, in fact, be the largest that could be obtained by an economically independent industry. While such a procedure would result in a greater supply of fish to the consumer, economic conditions in the fishing industry would, in other respects, be indistinguishable from those in an unregulated fishery. Conversely, it is well enough realised that the greatest catch per unit effort—and, roughly, the greatest rate of profit—is obtained by one ship alone exploiting the stocks (see e.g. Graham, 1951a, p. 22), but of course the total yield in such circumstances is minimal.

Thus we reach the conclusion that with a rationally adjusted fishing activity, i.e. with eumetric fishing, not only is it impossible to maximise both yield and working efficiency together, but if one is maximised the other is automatically minimised: it is difficult to visualise a situation in which either extreme would be acceptable as an objective for regulation, either to the industry or to society. We can find no peculiar virtue in conservation for its own sake, and believe that as a general principle it is misleading to regard conservation and economic management as two separate and independent functions of regulation, especially as to do so apparently leads, as we have shown, either to the former being regarded as obligatory and the latter voluntary or, at least, to the former being assigned the greater weight on principle. Rather, we would suggest that fishery regulation should be conceived on a broad enough basis to embrace biological, economic and social factors on, *a priori*, equal terms; it should have as its general objective the adjustment of these factors so that in each particular case the best balance is achieved between the benefits on the one hand to the producer, in the form of profit to the fishing industry and a good living for fishermen, and on the other to the consumer, as a large and steady supply of fish at a reasonable price. This best balance we shall call a state of *optimum fishing*, and in what follows we discuss in more detail the economic factors that enter into a determination of the requirements for it.

19.1.3 *Some economic considerations*

With eumetric fishing there is only one primary independent variable that can be adjusted to achieve optimum fishing as defined above, namely the fishing mortality coefficient, F, or in effect, the fishing intensity. The relationship between this and the weight of yield is expressed by the appropriate eumetric yield curves, such as those of Figs. 19.2; there remains for consideration the associated changes in economic conditions, which depend primarily on the profit of fishing, that is, the difference between the total value of the catch in monetary units and the total cost of fishing, including overheads such as the maintenance of vessels, shore establishments and so forth.

The analysis and prediction of values and costs is, admittedly, a complex problem, but we do not share Burkenroad's (1953) belief that such quantities are largely intangible. Certainly, the attainment of a state of minimum—or even zero—profit has been tangible enough in many fisheries, and resulting conditions have been reasonably stable. In the North Sea demersal fisheries economic factors have resulted in very similar steady states being reached after both world wars, despite the economic upheaval and enormous changes in the purchasing power of money caused by them. Evidence such as this suggests that there may be factors in the economy of major commercial fisheries that are perhaps rather more consistent and more predictable than in some other commercial undertakings. Nevertheless, it cannot be denied that understanding of the economics of fisheries lags behind that of their biology. This is not only because nearly all workers who have been concerned with fishery regulation have been biologists by training but also, we suggest, because of the widespread tendency to associate regulation with biological conservation to the exclusion of economic management. It is perhaps not without significance that the most comprehensive investigation of fishery economics to date has been undertaken by someone who is opposed to regulation of any kind (Taylor, 1951).

From the foregoing it follows that the main requirement for an economic assessment of the kind we have in mind is to deduce the form of the relationships between the fishing mortality coefficient F and the total cost of operating the fleet that generates it, and between the weight of the annual yield and its value. For the moment we express them as general functions ϕ' and ϕ'' of the fishing mortality coefficient and yield respectively by writing

$$\text{Annual running costs (including overheads)} = \phi'(F)$$

$$\text{Value of the annual catch} = \phi''(Y_W)$$

We also retain the simplifying assumptions set out in §19.1.1, namely that we are dealing with a fishery based primarily on a single species and fished by a single fleet, to which we add here the proviso that the associated industry is economically dependent on the yield from that species alone. Since we are concerned with eumetric yield curves, the functions $\phi'(F)$ and $\phi''(Y_W)$ refer to steady states: implicit in them are therefore the assumptions that the shore organisations and docking facilities necessary to maintain the fleet, and the transport and marketing arrangements for dealing with the landings, are adjusted in accordance with the size of the fleet and the average annual catch.

19.1.3.1 *The relationship between fishing intensity and running costs*

We consider first the relationship between the magnitude of F and the cost of generating it, i.e. the function $\phi'(F)$. From the definition of fishing intensity given in §3.3, it follows that there are, broadly speaking, three different ways of changing F; (a) by changing the total number of vessels comprising the fleet, (b) by changing the time that each spends fishing per year, and (c) by changing the fishing power of each vessel, i.e. its size or the efficiency of its gear. The attainment of optimum fishing requires that any given value of F shall be generated with as much economy of time and money as is compatible with certain other factors that are discussed more fully in §19.1.4, although implicit in the concept is the maintenance of an adequate standard of wages and working conditions for fishermen and other members of the industry. In other words, general operating efficiency must be taken as a guiding—but not an over-riding—principle in achieving optimum fishing. Just such a view has, in effect, been advocated by Nesbit (1943) and Graham (1952), and it means that any desired value of F must be generated by adjusting, primarily, the total fishing power of the fleet.* We do not know of any published information on the costs of operating fishing fleets, but we may surmise that they are roughly proportional to the number of vessels engaged in fishing, and thus in turn, for vessels and gear of a given efficiency and for a given system of fishing (see §10.3), to the value of F generated by them. Therefore we conclude that with the system of regulation we are envisaging, the function $\phi'(F)$ is roughly one of proportionality, or possibly linearity with a relatively small constant term to cover certain shore installations that may be largely independent of the number of vessels comprising the fleet.

19.1.3.2 *The relationship between yield and value*

There is now the more difficult question of finding whether any generalisations can be made about the relationship between the annual yield and its value. This reduces, primarily, to deducing the effect of the volume of landings on the price of fish, i.e. its value per pound; but because we are referring, specifically, to yields lying on a eumetric yield curve there will be two other factors influencing the total value of the catch that are correlated with its magnitude in a predictable way, namely, the size composition of fish comprising it and the extent of its natural year-to-year fluctuations. These three factors require separate treatment.

Taylor (1951) has made a comprehensive survey of economic statistics of some American fisheries, adjusting fish prices over a period of sixty years to allow for variations in the purchasing power of money. From this it appears that while in some cases there has been a tendency for the price of fish to vary inversely with its supply there have also been some notable exceptions to this rule. Thus the great increases in yield in the California sardine fishery after the first world-war were accompanied by a fall in its price index, while the price indices of fish from the Great Lakes fisheries rose considerably after 1921 when stocks were being depleted and the yield was falling. On the other hand, the landings of haddock from the Atlantic coast fisheries have increased by between three and four-fold since the beginning of the century, during which time its price index has remained virtually constant. Again, the production per head of Atlantic cod has fallen throughout the century, but its price index has not increased in response. The general impression gained from the data assembled by Taylor is that the price of fish is not greatly dependent on its production. Even in the California sardine, where the increases in yield seem to have been most pronounced and rapid, an increase of nearly 300% in the yield caused a fall of only 37% in price; while the apparent sensitivity of price to a decrease in yield of the Great Lakes

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*This must allow for improvements in efficiency of vessels and gear, which it is part of the function of the *method* of regulation to encourage. Again, other considerations may apply to regulation at the international level, and immediate adjustments of F may have to be carried out by varying fishing time. These matters are discussed in §19.2.1.

fisheries was in reality more the result of the demand for fish by a rapidly increasing human population.

The problem of establishing a working relationship between yield and price over that part of a eumetric yield curve that need be considered for regulative purposes may possibly involve rather fewer complications than are present in some of the cases examined by Taylor. Thus the need for an economic assessment to guide regulation will not usually arise until a fishery has at least been extensively developed and probably has reached a steady state at or near to the minimum profit level (i.e. has become 'overfished'). In such cases the range of yield that need be considered will not differ greatly from that which has already been experienced, and no great degree of extrapolation is called for. This can be seen from the position of the mean pre-war yields of plaice and haddock relative to the eumetric yield curves of Figs. 19.2; while in §20 we conclude that with the more limited regulation that is practicable as an immediate objective for the North Sea demersal fisheries as a whole, the best total yield that can be expected is of the order of 20% above the mean pre-war level. Since a major fish stock could hardly become seriously depleted unless there were an extensive consumer demand for its product, and remembering also that increases in yield resulting from regulation are predictable and can be spread out over as long a period as desired, it does not seem unreasonable to suppose that in the majority of the fisheries needing regulation, market research and improved transport and quality could allow increases of this order of magnitude to be made without a serious fall in demand or price. The course of events in the New England haddock fishery can perhaps be taken as a fair indication of what might be expected. Here, as Taylor points out, the increases in production were paralleled by continued technological developments in marketing and transport, including the introduction of filleting, packaging and freezing. These enabled demand and price to be maintained not so much by making the product more attractive to the original consumer near the ports, but by bringing the product in a reasonable condition to the enormous inland markets that had previously been untouched.

It can be said that fish is only a minor constituent of the protein diet in many countries. It comprised about 1/9th of the consumption of animal protein in Great Britain in 1946 (Beverton, 1948), and Taylor (1951) has shown that it is not an important source of protein even in some maritime states of the U.S. Yet fish has a character and appeal of its own; it is not usually an essential food, neither is it a luxury; as much as anything it is a means of introducing variety into the diet. Hence even when the supply of other protein foods is cheap and plentiful there is always likely to be a fair demand for fish, although the fact that it is not a staple food means that it would not be bought if the ratio of its price to that of competing foods tended to rise above a certain value. Fish as a source of variety in the diet, and the fact that often there are potential markets for fish that would not be saturated even if the fisheries supplying them were operating at maximum productivity are, we suggest, the key factors governing the relationship between supply and demand in the case of fish products. Although some tendency towards an inverse variation between the size of yield and the price of fish is to be expected, the above two factors taken together would seem able to restrict such variation to fairly narrow limits. Thus they provide a reasonable explanation of the conclusion which emerges from such data as are available, namely that price indices of fish seem in most cases to have remained relatively stable over a long period of years and despite major economic changes.

The variation of the annual yield due to fluctuations in recruitment, changes over a wide range along the eumetric yield curve. At low values of F and $t_{\rho'}$ the yield comes more or less equally from nearly all age-groups in the post-recruit phase and fluctuations are consequently highly damped; at the asymptote the whole of it comes from a single age-group and its variation is proportional to that of the recruitment itself. Fig. 19.5 shows the change in the coefficient of variation of yield along the plaice eumetric yield curve P(a) of Fig. 19.2.1, with the pre-war value shown by the point P. This curve is calculated from (6.31), using the true variance of plaice recruitment estimated in §15.2.2. Usually, a supply of fish will be worth more if it is regular than if it is irregular, but much depends on local conditions. Thus Herrington (1946) has shown that while quarterly landings of New

England haddock were inversely related to price, there was scarcely any correlation between yearly landings and the yearly mean price. This was because of a tendency for the size of the annual yield to be adjusted according to the price of competing foods; when the latter was high, landings of fish (rather than their prices) were increased, and vice-versa. It suggests the possibility that for maximum efficiency it may be necessary to frame regulative measures so that fishermen can vary their effort within limits to take best advantage of fluctuations in the price of competing foods (see §19.2.1).

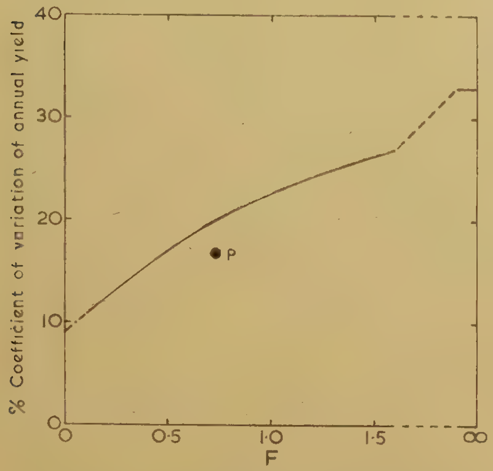

FIG. 19.5 PLAICE: VARIATION OF ANNUAL YIELD AGAINST FISHING MORTALITY WITH EUMETRIC FISHING

[Coefficient of variation of annual yield as a function of F with eumetric fishing, corresponding to eumetric yield curve P(a) of Fig. 19.2.1. The point P shows the pre-war value of the coefficient.]

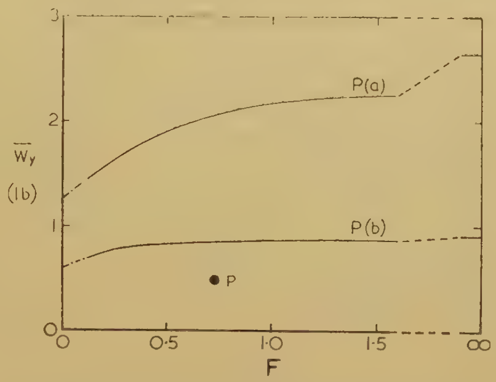

FIG. 19.6 PLAICE: AVERAGE SIZE OF FISH AGAINST FISHING MORTALITY WITH EUMETRIC FISHING

[Mean weight of fish in the catch, $\bar{W}_Y$, as a function of F with eumetric fishing, corresponding to eumetric yield curves of Fig. 19.2.1. Curve P(a) constant parameters; curve P(b) growth density dependent. The point P shows the mean pre-war value of $\bar{W}_Y$.]

The third factor influencing price that is associated with changes in yield along a eumetric yield curve, is the size composition of the catch, a useful index of which is the mean weight, $\bar{W}_Y$, of fish in the catch. The changes in this characteristic along the eumetric yield curve can be calculated in the usual way since the required values of F and $t_{p'}$ (or mesh size) are known from the appropriate eumetric fishing curve (e.g. Figs. 19.4). For comparison with observed values of $\bar{W}_Y$ it is, however, essential to use a theoretical model taking into account the density dependence of growth. This can be seen from the difference between the $\bar{W}_Y$ curves P(a) and P(b) for plaice shown in Fig. 19.6, which are calculated with constant and density dependent growth respectively and correspond to the eumetric yield curves P(a) and P(b) of Fig. 19.2.1. Apart from the difference in level between the two curves, it will be noted that curve P(b) is nearly horizontal throughout its range with only a slight tendency to fall at very low values of F. The pre-war value of $\bar{W}_Y$ is shown, as before, by the point P.

The extent to which variation in the size of individual fish affects its price per lb. could, in most cases, be established without difficulty from market statistics. It would be expected that the smallest fish would fetch the lowest price because their edible fraction is lowest (see e.g. Thursby-Pelham, 1932), but the converse is not necessarily true. Thus in all five species for which the price per lb. in each category is given in the English Statistical Tables (cod, haddock, hake, plaice and sole)*, the category 'medium' fetched the highest; the price in the category 'small' being between 25% and 50% lower, and that in the category 'large' about 10% lower. The 1951 price data for plaice plotted against the

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*E.g. *Sea Fisheries Statistical Tables* 1951, Min. of Agr. & Fish., H.M.S.O., 1952. Data for 1946 to 1950 inclusive are not strictly valid in this connection since price control was in operation.

average weight of fish in each category is shown in Fig. 19.7, from which it appears that the highest price per lb. is fetched by fish of a little over one pound in weight—not far from the limit to which the $\bar{W}_Y$ curve P(b) of Fig. 19.6 is tending. The slightly lower price of fish in the category 'large' in these instances is probably due to a combination of factors such as inconvenience of size for serving in restaurants and hotels, toughness of flesh and the high proportion of large spent fish in poor condition at spawning time.

A rough idea of the change in average price of fish along a eumetric yield curve can be obtained by multiplying the predicted mean weight $\bar{W}_Y$ by the corresponding price per lb. estimated by interpolation from a curve such as that of Fig. 19.7. Where the price of fish does not increase steadily with its size, as in the examples mentioned above, it may be necessary to predict the price change more accurately by estimating the size composition of the catch—in the appropriate market categories—at each point on the eumetric yield curve, and to compute an average price using the price per lb. in each category as weighting coefficients. It is important to note in this connection that although the mean weight of fish in the catch is unlikely to change much along a eumetric yield curve, the range of size of fish caught will vary considerably, decreasing as F increases. In cases where medium sized fish fetch the highest price, the average price of fish in the catch will change more than would be expected from the curve of $\bar{W}_Y$. Taking the variation of size composition into account may also be important where filleting or freezing processes are employed that can deal only with a restricted range of size of fish.

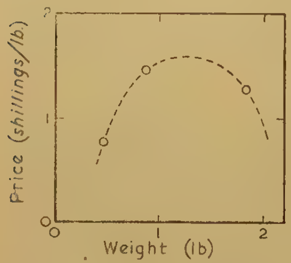

FIG. 19.7 PLAICE:
RELATION BETWEEN PRICE AND WEIGHT OF FISH
[Price per pound plotted against average weight of fish in each market category in 1951.]

19.1.3.3 *The direct effect of costs on price*

Before concluding this brief resumé of factors influencing the transformation of a eumetric yield curve to its value—cost equivalent, there are certain other points that must be mentioned. One of these is the possibility that the price of fish will depend to some extent not on any characteristic of the yield itself but on the cost of catching it. This is, of course, a well known property of many productive systems, and Burkenroad (1953) has suggested that it will be found in fisheries also. However, if increasing costs have had any effect on price in fisheries that have become overfished it has not been enough to prevent the profit margin from becoming negligible. Moreover, the usual incentive for reducing prices if production costs can be decreased is to stimulate consumption—and hence production and ultimately total profit—at the expense of competitors who have not reduced prices. But such an incentive could hardly exist in a satisfactorily regulated fishery, simply because with optimum fishing something near to the biological limit of production will already have been reached. We are not suggesting that no reduction in the price of fish would be made if a substantial decrease in production costs were achieved by means of regulation of effort. On the contrary, provision of fish at a reasonable price to the consumer is one of the criteria of optimum fishing as defined in §19.1.2, and price reduction is one way of absorbing some of the increased profit that would result from regulation: what matters here is that there will not necessarily be an automatic fall in price with decrease in the cost of fishing, and profit can legitimately be estimated in the first instance without taking this factor into account.

Both Taylor (1951) and Herrington (1946) discuss the effect of trends and fluctuations in the price of competing foods, especially protein rich ones, on that of fish. These constitute the 'economic environment' of a fishery; they have a relevance to the problem of establishing a working relationship between value and cost analogous to that of changes in the physical and biotic environment of a fish population in determining the eumetric yield curve as a function of fishing intensity. More directly important, however, are changes in the price of materials, fuel and general 'overheads' including wages, that determine the cost of generating a given fishing mortality coefficient, i.e. that are incorporated in the function $\phi'(F)$. The effect of these on the economics of fisheries does not appear to have been investigated in detail, but such changes in them as are a reflection of a fundamental trend in the cost of living and purchasing power of money affecting the price of fish in the same proportion, have no direct bearing on the economic state of a fishery because both functions $\phi'(F)$ and $\phi''(Y_W)$ are altered in the same ratio. Hence some of the undoubted difficulty of predicting future trends in real prices can be avoided, because it is only those factors affecting *differentially* the functions $\phi'(F)$ and $\phi''(Y_W)$ that could alter the requirements for optimum fishing. In this connection it is important to remember that there is no fundamental difference in their effect on the economic state of a fishery between an increase in the price of fish relative to the costs involved in generating a given fishing intensity, and an increase in the level of recruitment to the stock: the requirements for optimum fishing are changed in a similar manner in both cases, and in both an economic assessment is needed to establish how regulation of the fishery should be changed to maintain optimum fishing.

This discussion of the various factors involved in transforming a eumetric yield curve to its value and cost equivalent can be summarised as follows. Assessment of the relationship between the fishing mortality coefficient and the cost of generating it should present no particular difficulties. It can probably be taken as proportional, to a first approximation. Converting yield to value is essentially a matter of determining how the price of fish is likely to vary with yield along a eumetric yield curve. There are two factors tending to make price vary inversely with yield; (a) the size of the yield itself, and (b) the magnitude of the annual fluctuations in yield, which increase as yield increases. There is one that tends to make price vary directly with yield, namely the average size and range of size of fish in the catch. We suggest that the combined effect of these three factors, together with certain special features of the supply-demand relationship in the case of fish, would usually result in price remaining fairly constant over a wide range of a eumetric yield curve, with probably some tendency towards a limited inverse variation with yield.

19.1.4 *The eumetric value-cost curve and its relevance to the more detailed requirements for optimum fishing*

It follows from the above conclusion that unless special circumstances are involved, both functions $\phi'(F)$ and $\phi''(Y_W)$ can be regarded as ones of rough proportionality. Hence the transformation of a eumetric yield curve into its value-cost equivalent does not involve any fundamental change in its shape; that is to say, the eumetric value-cost curve also ascends asymptotically to a finite limit as cost increases. Curve (a) of Fig. 19.8 shows a hypothetical example of such a curve, based on the general shape of those of Figs. 19.2, in which it is supposed that total value and total cost are each expressed in monetary units and drawn to the same scale. This we use below to show how certain economic assessments necessary for determining the requirements for optimum fishing may be made.

Before proceeding, we must consider briefly the implications arising from the fact that we started, in §19.1.1, by treating yield and fishing intensity as the primary variables for developing the concept of eumetric fishing, and have derived the eumetric value-cost curve by a subsequent transformation of the eumetric yield-intensity curve. The exact method of deriving a eumetric value curve is, of course, to construct first a *value-isopleth diagram* by expressing each point on the original yield-isopleth diagram* in terms of the co-ordinates of value and cost, taking into account the various factors discussed above (i.e. the effects of size of yield, its fluctuation and the size composition of the catch). A curve can then be defined on such a diagram exactly analogous to the line BB′ on a yield-isopleth diagram (e.g. Fig. 17.14) and specifying, for any given cost of fishing, the

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*For this purpose the yield-isopleth diagram should be expressed in absolute yield, not in yield per recruit, in order to take account of the effect of size of yield on the price of fish.

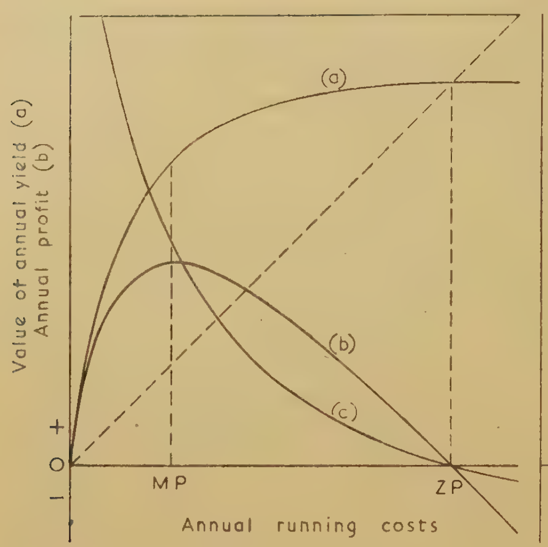

FIG. 19.8
EUMETRIC VALUE—COST CURVES

[Curve (a) is a hypothetical example of a eumetric yield curve transformed to its economic equivalent of value of annual yield plotted against total annual running costs. From this are derived curves of total profit (b) and profit per unit capital outlay (c) as functions of running costs.]

mesh required to produce a yield of the greatest total value. We have not introduced this complication at any earlier stage because it is essentially a technical refinement that does not involve any new concept. For a single species the difference between the true eumetric value-cost curve constructed in this way and one derived directly from a eumetric yield curve will usually be slight, except possibly at very low values of F where the eumetric yield might include some fish too small to be marketable. Since it would not benefit the value of the catch to reduce the size of mesh to such an extent that it results in the capture of appreciable quantities of fish too small to be marketable, it follows that in such cases the true eumetric fishing curve (i.e. that corresponding to the true eumetric value curve rather than the eumetric yield curve) would not extend below the mesh size whose 50% point corresponded to the minimum marketable size of fish. A combined value-cost curve for several species cannot, however, be constructed from the corresponding combined eumetric yield curve, and in such cases derivation from a combined value-isopleth diagram is essential (see §19.1.5).

Returning now to the eumetric value-cost curve of Fig. 19.8, the *total profit* to the industry can be derived at once as the difference between total value and total costs, i.e.

$$\phi''(Y_W) - \phi'(F)$$

and is shown as a function of $\phi'(F)$ by curve (b). It will be noted that the industry shows a profit wherever curve (a) lies above the bisector of the angle between the axes, that is, wherever the quantity $\phi''(Y_W) - \phi'(F)$ is positive. In theory, this criterion would not necessarily be satisfied anywhere on the curve, as might be the case if the exploited area was a great distance from port so that costs were very high, or if the density of fish was extremely low; in such circumstances, of course, a self-supporting industry could not exist. We are concerned with cases in which curve (a) lies above the bisector over a certain range of F, as we have indicated in Fig. 19.8, and from its general form it follows that the profit curve (b) will always have a maximum, and reach zero at some higher value of $\phi'(F)$—where, in fact, curve (a) crosses the bisector (ZP in Fig. 19.8). While the principle of eumetric fishing does not lead to a yield curve that has a maximum, we find that there is nevertheless a certain fishing intensity that will enable the industry to operate with the greatest margin of total profit, and it is necessary to examine the relevance of this to the requirements for optimum fishing as set out earlier.

The fishing intensity giving maximum profit is such that at any higher intensity the increased cost of fishing would outweigh the additional value of the catch, while at any lower intensity the reverse would happen; the point of maximum profit (MP in Fig. 19.8) is therefore where the eumetric value-cost curve has a slope of 45°. Thus it corresponds exactly to what Huntsman has proposed as the aim of regulation—"The take should be increased only as long as the extra cost is offset by added revenue from sales". (1951, p. 169). Again, though in a different context, Yates (1952) has used the term 'optimum' for what we have called the point of maximum profit. Dealing with the economics of fertilising crops he argues that if the whole of a crop is to be treated alike (cf. the exploitation of one species of fish by a single fleet, as we are considering here), the most economic level of dressing is that at which the cost of adding a further small increment exactly equals the value of the resultant average increment in response*.

From these interpretations it can be seen that the maximum total profit point offers the simplest objective compromise between maximising the value of the yield and minimising the cost of fishing. However, the economic significance of total profit depends very much on the structure of the fishing industry, and, in particular, on whether regulation of fishing intensity would involve changing the number of commercial units making up the industry (i.e. fishing companies or trawler concerns) with the size of each remaining constant, or the converse, since it is the profit to each such concern that is critical, rather than the total profit to the industry as a whole. Only if the number of units remains constant, and each receives a constant fraction of the total profit, will the profit to each unit reach a maximum when the total profit is maximal. At the other extreme is the type of fishing industry in which each vessel is separately owned, and there are no major commercial units that can vary in size. Here it is the profit to each owner—i.e. that earned by each vessel—which is significant, and the average of this is the total profit divided by the number of vessels. Now since, in the present context, adjustment of the fishing mortality coefficient by regulation involves primarily adjustment of total fishing power, it follows that with an industry of this type the value of F is approximately proportional to the number of vessels operating, and we can represent the relationship symbolically as $\phi'''(F)$. Hence the relevant profit curve in such a case is not that of total profit to the industry but of profit per vessel, i.e. the function

$$\frac{\phi''(Y_W) - \phi'(F)}{\phi'''(F)}$$

This, when plotted against $\phi'(F)$, gives a curve that descends continuously from a large positive value at $\phi'(F) = 0$ (strictly, at the value of $\phi'(F)$ when only one ship is operating) to zero when the total profit becomes zero. An example is shown by curve (c) of Fig. 19.8.

Although profit is the key factor determining the economic state of the industry there are, of course, other items that must be taken into account. While we cannot discuss these in detail it is worth mentioning one group, namely those that depend, directly or indirectly, on the total capital outlay; for example, the rate of interest that can be paid on money invested in the industry. A rough index for this purpose is the *profit per unit capital outlay*. Since capital outlay is itself roughly proportional to total fishing power, the curve of profit per unit capital outlay has a shape similar to that of profit per vessel, i.e. curve (c) of Fig. 19.8, and has no maximum. In cases where the total profit curve is shallow it is possible that even at its maximum the profit per unit capital outlay may not be sufficiently high to meet the standard required.

We can now formulate in more detail the concept of optimum fishing put forward in general terms in §19.1.2, namely that fishing which gives the best balance between the benefits to the producer and consumer components of the system to be regulated. Where total profit is of direct relevance (i.e. in the former type of industry mentioned above) the fleet and the industry when operating at the maximum total profit point would be the smallest that could efficiently generate the required value of F, and the resulting yield would be less—perhaps considerably less—than that which could be obtained if the industry operated at the smallest profit margin that permitted economic stability; moreover, the price of fish would be as high as permitted by consumer demand. Clearly, these conditions are not necessarily optimal for the system as a whole. For example, a nation's immediate need for fish as food may be great enough to justify a fishing intensity higher than that giving maximum profit; and in the extreme case, in order to obtain the greatest possible supply of fish, the optimum fishing intensity may be higher even than the zero profit point. Another factor that may demand a fishing intensity greater than that giving maximum profit is the need to keep the fleet larger than would otherwise be necessary, either to provide a reserve of ships and seamen, or simply because fishing may be an essential industry from which it is impracticable or undesirable to divert men to other occupations. Considerations such as these imply that the actual profit obtained with optimum fishing would be rather less than the maximum; and it is perhaps better to refer to the latter as the maximum *potential* profit.

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*Yates suggests using the same financial considerations to determine the 'optimum' expenditure on developmental work in terms of the results obtained in increasing production, pointing out that there may often be a case for not going right up to the maximum response, since the returns from the last few increments of expenditure are small and resources could better be applied to other problems. This is exactly parallel with the argument that rather than attempting to obtain the maximum yield from any one species it would be more profitable to divert, where possible, some fishing effort to underfished stocks.

Exactly the same set of criteria apply to determining the requirements for optimum fishing with the second type of industry mentioned above, in which profit per vessel rather than total profit is the critical factor. The only difference here is that the lower limit to the range of fishing intensity within which the optimum lies is not defined by the maximum potential profit point, and a fishery of this kind presents the essentials of the differences between biological conservation and economic management in their simplest form. There are, in fact, only four primary factors involved in the regulation of such a fishery, (a) the quantity of fish supplied to the consumer, (b) its price, (c) the number of fishermen and vessels engaged and (d) the profit to the individual owner-fisherman. Apart from maintaining eumetric fishing, regulation in this case involves ultimately, adjustment of the number of vessels so that the most acceptable compromise is obtained between these four inter-related factors, and no general statement can be made about where the optimum lies.

This, then, is our conception of optimum fishing and of some of the more important factors involved. Obviously, many of the latter are essentially matters of administrative policy of which further discussion is entirely outside our brief; we mention them here only to give perspective to what, in our view, is the range of factors that must, at one stage or another, be considered in achieving optimum fishing. How many of these factors would actually be the subject of legislation, especially when regulation is first undertaken is, of course, another matter. Certainly, we do not wish to give the impression that a complete and accurate assessment of either the economic and social, or for that matter the biological, components of the system is essential before any progress towards optimum fishing can be made. In many unregulated fisheries depletion may have gone so far that substantial improvements could be made by regulation before action becomes at all critically dependent on the more complex economic and biological inter-relations discussed in this section; we shall show in §20 that this is the case in the North Sea demersal fisheries. Nevertheless, the choice of regulative method is itself conditioned largely by economic and social factors, as is discussed further in §19.2.1; no kind of regulation can avoid altering them to some degree, and even a decision not to regulate at all involves, in most cases, the tacit acceptance of something approaching minimum economic efficiency in the fishing industry.

19.1.5 *Some practical complications*

The whole of our discussion has hitherto been confined to the case of a single species fished by one fleet or by a group of fleets which, for purposes of regulation, can be treated as one. We have also supposed that the fishing mortality coefficient and the age at which fish enter the exploited phase are independent variables that can be adjusted, over as wide a range as is desired, by regulation of fishing intensity and gear selectivity. We must now review briefly some of the more important ways in which actual fisheries can differ from this simple example which we have taken to develop our concept of optimum fishing.

19.1.5.1 *Interdependence of fishing intensity and gear selectivity*

In the first place there is the possibility that a change in gear selectivity may alter slightly the fishing power of the gear as a whole, in which event the parameters F and $t_{\rho'}$ would no longer be independent. Such evidence as is available (see §14.3) suggests that the effect is possibly unimportant except with large changes in mesh, but in so far as it exists it will mean that the relationship between F and fishing intensity for a eumetric yield curve must include a factor for mesh size. Since experience shows that an increase in mesh size tends, if anything, to increase the efficiency of the gear, the result will be to enable a given change in F—in either direction—on a eumetric yield curve to be brought about by a rather smaller relative change in number of vessels or fishing time. Clearly, this complication is of technical relevance only, and in no way affects the concepts of eumetric and optimum fishing.

19.1.5.2 *Limitations to the possible range of gear selectivity—restricted eumetric yield and fishing curves*

Another way in which an actual fishery may depart from the example we have been considering is that it may not be possible to vary the magnitude of $t_{\rho'}$ over the full range needed to satisfy the requirements for eumetric fishing. This complication has already been encountered in plaice, where it is found that for values of F less than about 0·1 the eumetric value of $t_{\rho'}$ is lower than the age at recruitment, t_ρ (see §19.1.1). Here it is a biological characteristic of the plaice population that sets a lower limit to the practical range of $t_{\rho'}$; an extreme case of this is probably provided by a fishery such as that based on species of Pacific salmon (e.g. the Fraser River fishery), where each year-class is available for capture on one occasion only during its life. On the other hand, it may be that the selectivity of the gear cannot for technical reasons be varied over a sufficient range. This is unlikely to be the case with trawls or seines, which lend themselves particularly well to variation of selectivity by alteration of mesh size, though it may be necessary to compensate for the reduced strength of particularly large-meshed gear by the use of thicker twine. However, it may be much less easy to alter, in a predictable way, the selectivity of some other types of gear, such as those in which fish are caught by hook.

Wherever one or other of the above factors sets a practical limit to the range of $t_{\rho'}$, that lies within the theoretical eumetric range of this parameter, it means that truly eumetric fishing is possible only within a certain range of F. Outside this there is no option but to leave $t_{\rho'}$ constant (at the highest or lowest value possible, as the case may be); the resulting yield curve we call a *restricted eumetric yield curve*, and it may be transformed into a value-cost equivalent and used as the basis for determining the requirements for optimum fishing just as if it were a true eumetric curve over its whole extent. There is, however, one possible difference between restricted and true eumetric yield curves, namely that while the latter always tend asymptotically to a finite limit, the former may have a maximum within the working range of F. The extreme case is when $t_{\rho'}$ is small and cannot be varied at all, which may result in yield curves of the kind illustrated in Figs. 17.2 and 17.24, with a well-defined maximum at a relatively low value of F.

The determination of optimum fishing in such a case presents only one new feature, namely that any fishing intensity greater than that giving the maximum yield is undesirable on both biological and economic grounds, simply because a lower fishing intensity would give a greater yield at a lower cost and an increased profit. Indeed, the only conceivable circumstance in which the optimum fishing intensity could be above that giving the maximum yield would be if the need to maintain as large a fleet as possible was great enough to outweigh all other considerations. Usually the optimum will lie on that part of the curve to the left of the maximum which, when converted into its value-cost equivalent, will be similar to and can be treated in the same way as a eumetric value-cost curve. Thus the maximum total profit point is, as before, where the value-cost curve has a slope of 45°, and hence will always correspond to a fishing intensity *less* than that giving the maximum yield; the latter is of relevance in fact only if biological conservation is taken as the sole basis for regulation, and we find ourselves unable to accept Van Cleve's (1945, p. 85) generalisation that "Fishery administrators must be concerned with the adjustment of the fishery to obtain the maximum yield". Clearly, the more steeply the yield curve ascends from the origin to its maximum, the nearer the maximum profit point is to the maximum yield and the more similar become the demands of biological conservation and economic management; but if the curve is at all flat-topped, obtaining the maximum yield may be so unprofitable that it is entirely impracticable as an objective for regulation.

19.1.5.3 *Fisheries based on more than one species –combined eumetric curves, uniform and composite regulation*

We now discuss briefly some of the special features that arise when the total yield to a fleet is made up of more than one species of fish. Where an exploited area contains several species of commercial importance that are caught simultaneously by the same gear and whose distributions are similar, regulation has to be applied uniformly to all of them, even though individually their requirements may differ. One possible procedure where *uniform regulation* of this kind has to be adopted is first to construct a combined value-isopleth diagram by summing the value of each species obtained by each pair of values of F and $t_{p'}$. This can be used as before to define a *combined eumetric value-cost curve*, at any point on which the magnitude of $t_{p'}$ is such that it enables the greatest combined value of all species together to be obtained, even though none of the pairs of F and $t_{p'}$ specified by it would produce a eumetric yield from any one species alone. From here onwards the determination of optimum fishing depends on the same kind of factors as have been discussed above.

It will be noted that with this procedure, maximum combined value is taken as the criterion of eumetric fishing, regardless of the relative contribution of the various species to the total yield. However, if there are marked differences in the dynamics of the species concerned (growth differences being especially important) it may happen that the *composition* of the total yield changes considerably along the mixed eumetric value curve. The most extreme case arises when only two species, or two groups of species, are present, of widely differing size with the larger capable of providing a yield of greater value (if fished with a sufficiently large mesh) than the smaller. Then, as F and $t_{p'}$ are increased eumetrically the proportion of the smaller species in the catch becomes progressively less until, at high enough values of F, it may be negligible, even though the value of the catch—now consisting almost entirely of the larger species—is greater than that of any mixed catch obtained at lower values of F and $t_{p'}$. In such cases an additional factor may have to be considered when determining the requirements for optimum fishing, namely the need to preserve some degree of variety in the yield, especially if the smaller species are exploited by one particular section of the industry. This can be met by setting an appropriate lower limit to the relative or absolute abundance of the smaller species in the catch, and constructing a combined eumetric value curve with this restriction imposed. This is another type of restricted eumetric curve, and has obvious affinities with that defined in §19.1.5.2 above for a single species, but differs in that no direct restriction is imposed on the permissible range of $t_{p'}$. An important similarity, however, is that both types of restricted eumetric curves can have a maximum at a relatively low value of F. Uniform regulation of the North Sea demersal stocks provides a good example of restricted eumetric curves, and a fuller discussion will be found in §20.2.

It may be noted here that if the distributions of certain species differ sufficiently the best results would, in theory, be obtained by *composite regulation*, in which each major stock is fished with a combination of fishing intensity and mesh size that is eumetric for it. The difficulties of composite regulation are largely ones of enforcement, and for further discussion the reader is referred to §20.1.

19.1.5.4 *Fishing areas exploited by more than one fleet—equivalent regulation*

In many exploited areas—including the North Sea—the fishing effort is *heterogeneous* as defined in §8.1.3; that is, two or more fleets associated with independent industries and of differing nationalities are operating, and may be using gear with differing selective properties. While the concept of eumetric and optimum fishing are still applicable in a general sense, additional factors may have to be taken into account in arriving at the most suitable form of regulation for the area as a whole. Examples include the need for maintaining some generally acceptable balance between the fishing activities of the nations concerned and the framing of regulative measures so that each nation makes an appropriate contribution to the overall regulation, especially if the selective properties of the gears cannot be made the same. The special problems raised by heterogeneous fishing and the need for *equivalent regulation* of this kind are discussed more fully in §19.3.

19.1.6 *Summary: review of existing definitions of optimum fishing and overfishing, and some proposed modifications*

The practical complications reviewed above show that in the regulation of more complex fisheries certain additional factors may have to be taken into account that are not present in the fishery based on one species which we considered previously. In such cases regulation may have to be rather more of a compromise between conflicting interests, but the concept of eumetric fishing and the objective of optimum fishing we believe to remain the basis of efficient regulation. By way of summarising our discussion of the principles of fishery regulation we therefore complete the review of existing ideas and definitions of terms such as 'optimum catch' and 'overfishing', to which some reference has been made earlier in this section.

We mentioned in §19.1.1 that Herrington, Nesbit and Ricker have used the term optimum catch to mean that which would be obtained by catching all fish of each year-class as soon as this reaches its greatest total weight. Thus the optimum catch as defined by these authors is identical to what we call the asymptotic catch—i.e. the upper limit of the eumetric yield curve—for the case in which the parameters of recruitment, natural mortality and growth are constants. These authors also refer to the size at which fish must be caught to give the optimum catch as the 'optimum size', and regard this as the size at which the increases in total weight of a year-class due to growth are exactly balanced by the decreases due to natural mortality. We have shown in §19.1.1, however, that the concepts of optimum catch and optimum size thus defined are no longer valid when the density dependence of parameters—particularly of recruitment—is considered.

A number of other authors, notably Hjort, Jahn and Ottestad (1933), Graham (1935, 1939, 1948) and Baerends (1947) have used the term optimum catch in a different sense, identifying it in effect with the maximum value of a curve of equilibrium yield as a function of fishing intensity in which the age at entry to the exploited phase is either not mentioned specifically or is taken as constant. This definition has usually been arrived at by means of the sigmoid curve theory (see §17.8), but we have found that the presence of a maximum in a yield curve cannot be regarded as a general feature and depends critically on the magnitude of $t_{\rho'}$ as well as of the parameters of natural mortality and growth. Graham and Baerends, and also Russell (1942), speak of rational fishing as the particular amount of fishing that enables this maximum catch to be obtained.

All the above authors therefore agree in defining the optimum catch as a maximum catch in a steady state, but the maximum referred to by the former group, in which variation in the age at entry to the exploited phase is taken into account, is not the same as that defined by the latter, in which this factor does not appear. Now, we have shown that to obtain the asymptotic catch (by adjusting both F and $t_{\rho'}$) would require an extremely high—perhaps even an infinite—fishing intensity, as indeed Nesbit and Ricker clearly state: it is therefore unattainable in practice. Further, even when conditions are such that a maximum steady catch would be obtained at a reasonably low fishing intensity (e.g. with a restricted eumetric yield curve, especially if $t_{\rho'}$ were small and completely invariable) it would almost always be best for economic reasons to use a fishing intensity lower than that needed to give the maximum catch, to an extent depending on the degree of curvature of the yield curve in the region of the maximum. It does not therefore seem that the term 'optimum' is an appropriate synonym to 'maximum' in this context, since the maximum catch is seldom the 'best' but only the greatest; and whereas the maximum catch is determined purely by the biological characteristics of the fish population, the 'best' catch also takes account of the conditions under which it is obtained, and is therefore as much an economic and sociological concept. This is, in effect, the conclusion reached by Sette (1943b), who restricts the term 'optimum' to economic and social criteria, though because his use of it makes no specific reference to biological factors it does not include eumetric fishing as a prerequisite of optimum fishing.

The question of defining optimum fishing is obviously related in a general sense to that of defining overfishing, and some comment on the latter problem may not be out of place here. The term 'overfishing' has been used by many authors, but often no definition has been given and those that have been proposed differ considerably in detail and some are mutually contradictory. One approach has been to attach an analytical meaning to the word, defining it in terms of the balance of factors directly responsible for yield. Graham (1948) has reviewed the ideas of early writers such as Buckland and Petersen (1894), and modern analytical definitions of overfishing would seem to derive from the latter's statement of the requirements for obtaining the maximum yield, according to which the fishing should be adjusted so that it . . ."took exactly so much as the stock could reproduce by new growth". Thus according to Blackburn (1949), "Overfishing is any process of fishing that results in the total mortality losses, by the part of the stock that is useful to man, outweighing the accessions due to reproduction and weight increase of survivors". The limitation of this kind of definition is that it identifies overfishing with a departure from a steady state; it is, in fact, no more than a statement of the requirements for stability of total stock weight. It is clear from experience, however, that the harmful effects of excessive fishing can be manifest in a stable fishery, so that overfishing cannot usefully be defined in this way.

Another kind of definition is based on the symptoms of excessive fishing rather than on the factors responsible for those symptoms. Probably the simplest is Roelofs' (1951, p. 135) suggestion that a decline in catch per unit effort as effort increases is overfishing; but except in special circumstances (see e.g. §18.5.2) this decline will exist from the moment fishing begins (see Graham, 1951a). A more satisfactory and generally held definition, discussed in detail by Russell (1942), is that overfishing occurs when fishing has developed to a stage at which not only the catch per unit effort, but also the equilibrium catch itself, declines. Clearly, this originates from the premise that the existence of a maximum at a relatively low intensity is a general feature of equilibrium yield curves, and is thus open to the same limitation noted above in connection with the identification of the optimum state with such a maximum, namely that the latter may not exist if variation in the age at entry to the exploited phase is taken into account. It also implies that overfishing is entirely biological in origin, because even obtaining the maximum yield may be completely unprofitable (see §19.1.5); yet exclusion of economic considerations is certainly not intended by many authors who have used this definition (e.g. Graham, 1935).

More recently there has been a tendency to make a distinction between 'biological' and 'economic' overfishing in an attempt to overcome this difficulty, but so far the latter has usually been defined as that amount of fishing which reduces the profit margin to nothing (e.g. Van Cleve, 1945; Idyll, 1952). It would seem equally legitimate, however, to describe as overfishing other conditions in which there was some profit but not as much as could result from a still better adjusted fishing activity. In view of these many different meanings, or shades of meaning, that have been given to the word, it is perhaps significant that in one of the most recent statements of the problem Graham (1951a) adopts the general definition of simply "too much fishing"—this involving biological, economic or any other relevant factors. In pointing out that "A more restricted definition might prevent something being done when it needs to be done; or might cause regulation when there is no need for it", he focuses attention on the essential criterion to be satisfied by a definition of overfishing, namely that the action implied by its use should be correct and unambiguous.

In these circumstances it may therefore be worthwhile to examine the problem of defining what is meant by overfishing from the standpoint of the definitions of eumetric and optimum fishing proposed earlier in this section. Since, according to these, the optimum fishing intensity must lie at some point on the eumetric fishing curve for the fishery in question, we can take a hypothetical example of such a curve, as shown in

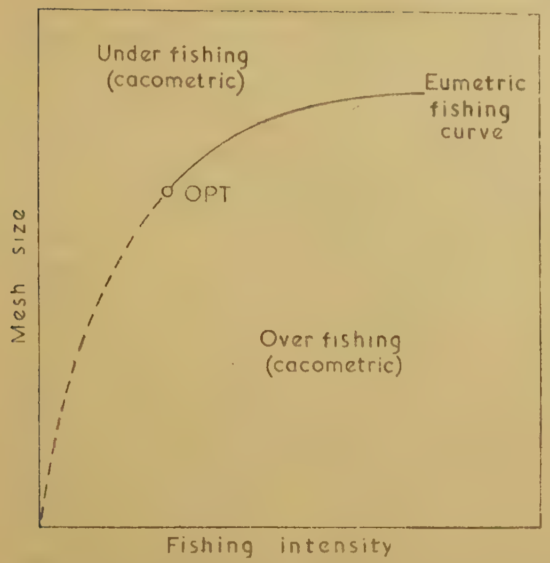

FIG. 19.9 DEFINITIONS OF OPTIMUM FISHING, OVERFISHING AND UNDERFISHING

[The curve is a hypothetical example ot a eumetric fishing curve, with the point of optimum fishing lying on it at OPT. Any combination of fishing intensity and gear selectivity lying on the broken part of the eumetric fishing curve below OPT is eumetric underfishing, while the continuous part above OPT defines eumetric overfishing. Any combination of fishing intensity and gear selectivity not on the eumetric fishing curve is called cacometric; if it is below, it is cacometric overfishing; if above, cacometric underfishing. See text for further explanation.]

Fig. 19.9, and suppose that the optimum intensity is at some point OPT. If, now, the concept of 'too much fishing' is extended a little to include not only a fishing activity that generates too high a fishing mortality in the stocks (i.e. too great a fishing intensity), but also one that causes the fishing mortality to operate on fish while they are still too young (i.e. too small a mesh size), it follows that any fishing activity that generates a pair of values of F and $t_{p'}$ lying below the eumetric fishing curve could legitimately be called overfishing. Consider, however, the effect of a fishing activity that is eumetric but that lies somewhere on the eumetric fishing curve above the point OPT. We have discussed in §19.1 how economic distress could come from operating at too high a point on a eumetric yield curve, although the steady yield there is greater—perhaps considerably so—than at the optimum. Therefore we suggest that fishing on a eumetric curve but above the optimum is just as much 'overfishing' as is fishing on the descending limb of a yield curve having a maximum. It may sometimes be necessary to distinguish between these two ways in which overfishing can arise, since although adjustment of fishing intensity and gear selectivity is required to reach the optimum in both cases, the emphasis is not the same on the other factors involved in regulation (see below). Hence we suggest that operating below the eumetric fishing curve could, if desired, be called *cacometric overfishing*, while operating on it but above the optimum could be called *eumetric overfishing*. Finally, *underfishing* is appropriately defined as the exact converse of overfishing, being similarly qualified as *cacometric underfishing* for any combination of fishing intensity and mesh size lying above the eumetric curve, and as *eumetric underfishing* for any combination which, though it lies on the eumetric curve, is below the point of optimum fishing.

These definitions may seem at first sight to depart from existing concepts, but some elaboration is clearly necessary to take account of the variation of both fishing intensity and gear selectivity, and we believe that they nevertheless retain the essential ideas that were originally intended to be conveyed. For example, when a fishery is first started the fishing intensity must increase from zero, but the gear selectivity will probably be such that all fish are retained above the minimum size that can readily be sold on the market. Although this will usually be smaller than that required for optimum fishing, the characteristics of the fishing activity must, initially, lie *above* the eumetric fishing curve (e.g. to the left of the broken line in Fig. 19.9). According to our definitions this would be underfishing (cacometric), which has the desired implication, namely that the main need is for expansion of the fishery rather than for any form of regulation—which in any case could probably not be adequately specified at this early stage.

The subsequent development of the fishery will be conditioned primarily by economic incentives, and typically the fishing intensity will increase until stability is eventually reached at the point where the profit margin has become insufficient to permit any further expansion. It is most unlikely, however, that this development will be accompanied by any increase in gear selectivity; in all probability this will be decreased in an attempt to maintain profitable fishing by developing a market for even smaller fish, and will eventually be forced down to the lowest practicable level. Thus it follows from our definition of eumetric fishing that the final steady state reached by an unregulated fishery will involve a pair of values of F and $t_{\rho'}$ lying *below* the eumetric fishing curve. This is overfishing (cacometric) according to our definition, and any progress from here towards optimum fishing must always call either for some increase in gear selectivity or decrease in fishing intensity, and probably for both. Hence our definition of overfishing implies, unambiguously, the need for conservative regulation as opposed to expansion, and is thus in harmony with Graham's (1951a) use of the word; at the same time it does not presuppose the exact form that regulation should take—a question that is better made the subject of a more detailed statement of the biological and economic characteristics of the fishery in relation to the requirements for eumetric and optimum fishing. The definition is also applicable to a fishery in which the value of $t_{\rho'}$ cannot be varied, and in which the yield curve might therefore have a maximum within the practicable range of fishing intensity, with the optimum at some point on the curve to the left of this maximum (see §19.1.5.2). The question of distinguishing between eumetric and cacometric fishing does not now arise, and any intensity greater than that at the optimum is overfishing, whether it lies to the left or right of the maximum.

It will be noted that our proposed definition of the word 'overfishing' does not distinguish between biological and economic considerations, since any form of fishing activity that is not optimal must involve, by definition, a maladjustment within the set of factors that can be called, broadly, economic and social, the best balance between which is the essential criterion of optimum fishing. Such a distinction can be made, however, by qualifying 'overfishing' as 'cacometric' or 'eumetric', according to whether both biological and economic factors or only the latter are maladjusted. For a similar reason all our definitions refer to the characteristics of the fishing activity and not, explicitly, to the resulting yield. Having abandoned the principle of obtaining the maximum yield as the objective of fishery regulation, the particular yield that would be obtained with optimum fishing is only one of several factors involved and has no special significance in itself. There are, indeed, many other combinations of fishing intensity and gear selectivity that would result in the same yield, but that which enables optimum fishing to be achieved is unique.

19.2 Attainment of the Objective of Optimum Fishing

In §19.1 we arrived at definitions of eumetric and optimum fishing in terms of the biological, economic and social characteristics of a fishery. Here we are concerned with the practical methods by which fisheries may be regulated to achieve optimum fishing (§19.2.1), and with events during the transitional phase between the time that regulation is put into effect and the attainment of the new steady state (§19.2.2). Finally, in §19.2.3, we discuss application of the statistical control chart technique to the problem of maintaining a regulated fishery in the optimum state.

19.2.1 *Methods of regulation*

During the course of time a number of methods for regulating a commercial fishery have been proposed, and their particular merits and demerits have been discussed in some detail by Herrington (1943), Nesbit (1943) and Baerends (1947) in papers to which reference has been made in §19.1. We therefore restrict our treatment here to discussing their relevance to the problem of achieving optimum fishing as we have defined it in §19.1.4.

A convenient summary of regulative methods is that given in the Final Report of the Standing Advisory Committee to the International Conference on Overfishing, 1947. Those recommended were intended primarily to apply to the North Sea demersal fisheries, but are fairly comprehensive and of wide application. Quoting from the Report, they are:

1. Minimum size of mesh.
2. Minimum legal size of fish.
3. Reduction of power of fishing fleets.
4. Reduction of catch.
5. Control of building of fleets.
6. Control of fishing activity.
7. Closed time.
8. Closed areas.

It will be noted first that proposals 1 and 2 refer to control of the age, $t_{p'}$, at which fish enter the exploited phase, while proposals 3-7 provide for direct or indirect control of the fishing mortality coefficient F. Proposal 8, closure of areas, can influence both parameters, as is explained below. Since eumetric fishing is a pre-requisite of optimum fishing, it follows that these two groups of methods are complementary and not alternative, and that regulating for optimum fishing must concern both. The main question is therefore one of deciding which method, or combination of methods, of adjusting the values of $t_{p'}$ and F is likely to be most effective and to produce results most nearly satisfying the requirements for optimum fishing. We consider first the methods for adjusting the value of F, i.e. proposals 3-8 above.

19.2.1.1 *Control of fishing intensity*

It will be remembered that for a given relative distribution of fish and fishing in a specified area the value of F is proportional to the total fishing effort, measured in standardised units of fishing power. Hence any regulative method that brings about a change in the fishing power of individual vessels and gear, the total fishing power of the fleet (e.g. its total tonnage), or the time spent fishing per year, will cause an approximately proportional change in the fishing effort and hence in the magnitude of F. Each of the proposals 3, 5, 6 and 7, therefore provides for the direct control of fishing effort, and to this extent are equivalent.

Reduction of catch (proposal 4) by setting a limit to the total catch that may be taken in a year, is an indirect method of controlling fishing effort. It is indirect because the catch obtained in a particular year by the expenditure of a given effort is influenced to a greater or lesser extent by biological factors, of which fluctuations in recruitment and, especially for migratory fish, in the distribution of fish, are the most important. Hence, although regulation by catch limits may be administratively simple, it affords no precise control of the magnitude of F.

Closure of an area to fishing, proposal 8, can operate in two ways. If the area closed is a nursery ground the effect is primarily to increase the age at entry to the exploited area, i.e. the value of t_p; if this higher value of t_p is greater than $t_{p'}$, i.e. if closure protects young fish that would otherwise be liable to capture by the gear in use, then the method is equivalent to an increase in gear selectivity (see §19.2.1.2). Closure of part of the area occupied by the adult population, on the other hand, decreases the effective overall fishing intensity, $\tilde{f}$, because it causes the distribution of the same effort to be less efficient (see §10.3). There is, however, no simple way of estimating the effect of closure on the magnitude of $\tilde{F}$, since it depends primarily on the rate and pattern of interchange of fish between the closed area and that open to fishing. With a very rapid rate of interchange, closure would have virtually no effect, while with a very slow rate closure would amount simply to reducing the number of recruits to the exploited phase, and would therefore be harmful. The example illustrated in Fig. 18.23 is intermediate, but even here the benefit of closure is slight. It is evident that rather particular conditions would be required for closure to bring any appreciable benefit, and to assess it would need a full investigation of fish movements.

So far we have been concerned with the efficacy of the various regulative methods from the point of view of the control they afford of the magnitude of F (strictly, of $\tilde{F}$).

There are, of course, other practical differences between them, notably in the ease with which they can be enforced and in their economic and social effects on the structure of the fishing industries, and on the way of life of fishermen. These are matters largely of administrative policy, but there is one practical implication that greatly restricts the choice of method and whose importance does not seem to have been fully appreciated hitherto. Any progress towards optimum fishing from the state of minimum profits that characterises overfishing will, initially, make fishing more profitable. But profit is the prime motive governing the expansion of any commercial fishery. Therefore there will arise the incentive—and the means—to take advantage of this more profitable fishing by increasing the number and power of vessels operating—unless these factors are specifically controlled by regulation. In order to maintain the value of F at the desired level further restriction therefore becomes necessary, whether it be by limiting fishing time, the area open to fishing, the catch, or the fishing power of individual vessels and gear. Without control of number of vessels, stability can be reached only when the value of F has become so low that no further reduction can cause any increase in the profit of fishing: thus the economic end-product of any such regulation is again a state of minimum profits.

It so happens that just such a sequence of events has occurred in the first major fishery that was the subject of an extensive programme of regulation, i.e. the Pacific halibut fishery (see, e.g., Thompson (W.F.), 1950). Here, the setting of catch limits has been the only regulative method adopted, and it has enabled the fishing effort to be reduced to something in the order of one-third of its original value, the yield being some 25% greater. However, the greatly increased stock abundance and potentially greater profit of fishing has caused the number of vessels engaged to double; hence the fishing season, originally of some eight and one-half months in duration, has become reduced to between one and two months, i.e. to about one-sixth. If stability has by now been reached it is presumably because the cost of building more vessels, which may remain idle (and depreciating in value) for nine-tenths of each year, cannot be met from such small profit margin as remains; but if some further improvement in the efficiency of vessels or gear took place, enabling them to be operated more economically, there is no reason to believe that the size of the fleet would not increase still further and the fishing season have to become shorter still.

The question of whether the recent biological changes in the stock of halibut are, in fact, the result of regulation has been challenged by Burkenroad (1948, 1950). Although the critical evidence to test this is wanting, or at least has not been published, to ascribe changes of such a magnitude and timing to natural fluctuations is, in our view, stretching coincidence to an excessive degree (Holt, 1951). A more pertinent question, however, is whether the changes have been of the kind needed to bring the halibut fishery to an optimum state and, more particularly, whether on the basis of this experience of regulation by catch limits the method can be recommended for the North Sea demersal fisheries, as has indeed been proposed by Baerends (1947).

The fact that the average catch of halibut is now some 25% greater than before regulation can be taken as showing that regulation has succeeded in achieving some biological conservation, in the sense defined in §19.1.2. To this extent the consumer has benefited; but it is a moot point whether this benefit is not offset by the supply being restricted to such a short period each year. The retail markets for Pacific halibut are so far from the ports at which the fish is landed that facilities for preserving and transporting are well developed, and it may be that a glut of landings can be smoothed out before reaching the consumers. The majority of the markets for North Sea demersal fish are for fresh products, and here a glut would certainly be detrimental; in all probability the value of such a catch would actually be less than before, owing to temporary saturation of demand. It has also to be remembered that the halibut is probably not fished eumetrically; it is a line fishery and there has been no adjustment of hook size. Where eumetric fishing is possible a reduction of effort may not necessarily cause an increase in yield, e.g. if the change is from one point on the eumetric curve to a lower one.

Rather similar qualifications apply to the changes in fishing activity. While it is true that twice as many fishermen and vessels are engaged as before regulation, they are employed on halibut fishing for only one-sixth of the original time each year. Hence unless there is alternative employment such a change is scarcely beneficial to the producer. It is difficult to avoid the conclusion that the fleet is now operating much less efficiently than before, even to the extent that owing to the extremely short fishing season only the nearest and not the most productive grounds can be fished. When it is remembered that to this must be added the administrative cost of regulation, we again cannot see that such changes would be beneficial for the North Sea fisheries.

It follows from all this that the essential requirement for regulation of F to achieve optimum fishing is to maintain the profit margin at a desired level. This can be done only by limiting the total fishing power of the fleet in terms of the number of vessels operating and their total tonnage. We do not wish to imply that this should be the only regulative method that need be adopted; it would be so only if it was desired to obtain the maximum potential profit. In practice, as we suggested in §19.1.4, optimum conditions may require that a rather greater number of ships and men be permanently engaged than would otherwise be necessary to generate the required value of F, depending on the need to maintain an adequate reserve and on the scope of alternative employment. For this purpose some compensating reduction in the effectiveness of the rather larger fleet must be introduced to maintain the value of F required, and this could be done by limitation of catch, or fishing time, or areas, or gear efficiency. Which, if any, of these is chosen in addition to restriction of total fishing power is primarily a question of policy, but we would suggest for consideration that allocation of a limited number of fishing days per year to each vessel has much to commend it, both socially and economically. It would avoid gluts and temporary saturation of consumer demand, and leave fishermen free to distribute their working time over the year in the most effective way, having regard to seasonal variations in the abundance of fish and consumer demand, and to their own leisure time. The whole question of deciding the best method or methods of regulation, just as that of establishing the requirements of optimum fishing as the objective of regulation, is essentially a matter of administrative policy on how much of the potential profit is to be realised directly, and how the remainder, if any, shall be absorbed.

These conclusions refer primarily, of course, to the long-term regulative programme. Graham (1951a) has pointed out that even to stabilise total fishing power at its contemporary level would be beneficial as a first step in regulation, since it would involve making compensating reductions in total fleet size as the efficiency of vessels and gear increase, and thus allow the operator to obtain profit from new devices. When the stage is reached at which some actual reduction in fishing is needed, the allocation of a limited fishing time per year to each vessel again suggests itself as being a suitable method in the first instance, the permanent reduction in fishing power being made more slowly, perhaps by gradually discarding the oldest and least efficient vessels. Neither is it necessary for the details of regulation to be decided so definitely at the international level in the case of an area such as the North Sea in which a number of countries participate. Here, in order to distribute equitably the benefits of regulation among the countries concerned, it is necessary only to agree on fixed ratios of fishing effort; the details of how a limitation of effort is to be enforced are relevant only at the national level. Finally it should be noted that a regulative programme must take into account any other fisheries that can be profitably exploited as an alternative to those that are the immediate object of regulation, either for the whole or part of the year.

19.2.1.2 *Control of gear selectivity*

The regulative methods remaining for consideration are proposals 1 and 2, namely the institution of a minimum size of mesh and a minimum legal size for fish landed. We would stress at the outset that in a fishery based on a single species there would be no need, in theory, to institute a minimum size limit, since the correct mutual adjustment of fishing intensity and gear selectivity is sufficient to achieve eumetric fishing. Thus if it should be that the smaller fish do not command as high a price as the larger, or are of no commercial value at all, this factor would be taken into account when converting yield into value, and incorporated in the final eumetric value and fishing curves (see §19.1.4).

In practice, however, a size limit can be of value in helping to enforce a mesh regulation, and is indeed the only way of so doing if it is impracticable to inspect nets—preferably at sea while vessels are fishing. We are, of course, assuming here that fishermen would not voluntarily adopt the prescribed mesh. If they did, there would be no need for a size limit; but as a regulation mesh may well release large numbers of saleable fish, the temptation to use a smaller mesh is too great to neglect, especially in a large international fishery where it is virtually impossible to reassure a fisherman that all his competitors are adhering voluntarily to the regulation mesh. If a size limit is the only method of enforcement it must be such that the use of a mesh smaller than the prescribed size would serve only to increase the catch of undersized fish which could not be landed. Hence it must be set at or near the upper limit of the selection ogive of the regulation mesh for the fish in question, and is bound to involve the rejection at sea of great numbers of undersized fish. The wastage thereby incurred depends partly on the proportion of these rejected fish that survive, and this differs greatly according to the species concerned; in gadoid species, for example, it is unlikely that any appreciable number would survive, but in flatfish a fairly high survival rate may be possible with careful handling (see Min. Agric. Fish., Fisheries Notice, No. 25, 1937).

In the North Sea, size limits could be of value in enforcing the use of different mesh sizes for different species whose habitats do not overlap, or only overlap to a small extent. An example is the plaice and haddock, of which the former should be fished with a much larger mesh than the latter in order to achieve eumetric fishing on each. Even though both fish are often landed at the same port it might be possible to enforce a different mesh for each by means of appropriate size limits.

A size limit can also be used to enforce the closure of nursery areas to fishing. For this purpose the limit should be set near the upper limit of the recruitment ogive, thus encouraging the fleet to search for fish of the larger sizes and to avoid the nursery grounds. This is the function of the present size limit for plaice (25 cm.), which is a long way above the selection range of the present gear. Again, however, some wastage is inevitable, and if there is not a reasonably clear-cut spatial segregation of large and small fish it may be high enough to nullify the benefit of closure.

We mentioned at the beginning of this discussion on regulative methods that control of fishing intensity and mesh regulations are complementary. If a mesh regulation is enforced without control of fishing power, the more profitable fishing resulting from it will encourage the fishing power to increase until that profit margin is taken up. Control of fishing power is therefore necessary if it is desired to obtain the full economic benefits from a mesh regulation, so that the two methods of regulation are linked economically as well as biologically.

19.2.2 *Immediate effects of regulation—transitional phases*

When the appropriate methods of regulation have been decided upon there then arises the question of how they may best be put into effect. This problem involves economic and administrative considerations which are outside the scope of this paper, but there is also need to consider the changes that are likely to occur during the transitional period between the introduction of a regulation and the attainment of the new equilibrium. For example, an analysis of these transient effects may help to decide whether the desired fishing intensity and mesh size should be attained rapidly or slowly, separately or together—assuming all cases to be equally possible on other grounds. An exact prediction of the events during a transitional phase must, of course, be based on a knowledge of the contemporary age-composition of the population and, if possible, a prediction of the size of the year-class that will enter in the next year. In the following treatment it is necessary to assume a constant recruitment; the examples must therefore be regarded as illustrative only, but it is nevertheless possible to establish certain general conclusions that are of value.

19.2.2.1 *Regulation of fishing intensity*

We consider first the transitional phase following the introduction of a regulative measure causing a decrease in fishing mortality, and assume the selectivity of the gear remains unchanged. We base our example on plaice, and use the transitional equations of §8.2.1 with constant parameters. The conclusion reached in §18.8 was that $(F)_{\max}$ for plaice with the pre-war mesh size in use would be in the order of half the pre-war value, but we consider first a reduction of the fishing intensity to 75% of the pre-war value, this reduction taking place suddenly.

Thus putting $$F_0 = 0{\cdot}73$$

and $$F_1 = 0{\cdot}55$$

in (8.17) gives the annual yield in weight per recruit for each of the transition years following the change. These are shown by the open histogram in the lower part of Fig. 19.10, the change in the fishing mortality coefficient being indicated in the upper part of the figure. The following points may be noted:

(a) During the first year following the change in fishing intensity there is a big, and nearly proportional, drop in yield.

(b) The yield has almost recovered its original value by the third transitional year, and the loss in yield during this time is made up after seven years have elapsed.

(c) Although the new steady state is not theoretically reached until the λth year (in this case the eleventh), the changes occurring after about the sixth year are very small.

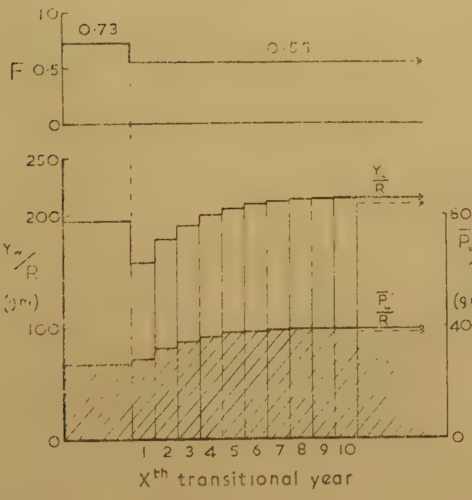

FIG. 19.10 PLAICE:

TRANSITIONAL PHASE FOLLOWING A REDUCTION IN FISHING INTENSITY

[Annual yield (open histogram, left hand scale) and catch per unit effort (shaded histogram, right hand scale) during transitional phase following a reduction of fishing intensity to 75% of the pre-war level in one stage, i.e. a sudden change in F from 0·73 to 0·55. Broken lines at the end of the transitional period show the yield (top line) and catch per unit effort (bottom line) for the new steady state calculated with growth density dependent. The horizontal line at the top of the diagram and the corresponding scale shows the time and magnitude of the change in F.]

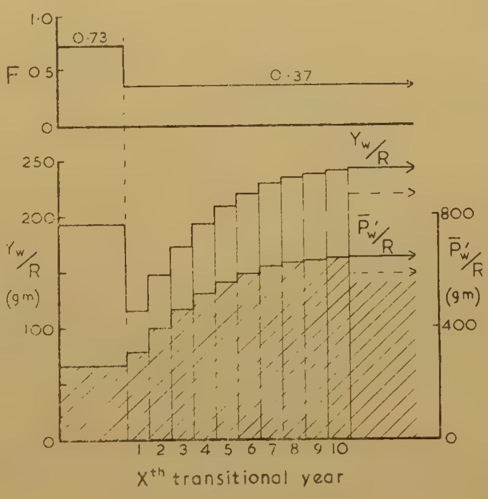

FIG. 19.11 PLAICE:

TRANSITIONAL PHASE FOLLOWING A REDUCTION IN FISHING INTENSITY

[Annual yield (open histogram, left hand scale) and catch per unit effort (shaded histogram, right hand scale) during transitional phase following a reduction of fishing intensity to half the pre-war level in one stage, i.e. a sudden change in F from 0·73 to 0·37. Other details as in Fig. 19.10.]

Fig. 19.11 shows the transitional phase corresponding to a reduction of fishing intensity o one-half of its pre-war value in a single step. In this case we have:

$$F_0 = 07{\cdot}3 \text{ as before}$$

but

$$F_1 = 0{\cdot}37$$

Comparison with Fig. 19.10 shows that the resulting initial fall in yield is more pronounced, that the original level of yield is reached during the fifth year, and the loss of yield is made up only after about nine years have elapsed. Finally, an effective steady state is reached after about eight years, although theoretically not until the eleventh, as before.

In addition to the yield, it is also necessary to know how the catch per unit effort changes during the transitional phase. This may easily be calculated in terms of the biomass of the exploited phase by dividing the yield in each year by the appropriate value of the fishing mortality coefficient for that year, and the resulting changes are shown by the shaded histograms of the above figures with reference to the right-hand scale. This gives the important result that the *catch per unit effort increases throughout the transitional phase.* The mean weight of fish in the catch, $\bar{W}_Y$, similarly increases throughout the transitional phase.

Before proceeding we need to make some appreciation of the effect of introducing certain of the more complex aspects of population behaviour discussed in Part II. The equations used to calculate the transitional stages of Figs. 19.10 and 19.11 assume a constant annual recruitment, which, in practice, would refer to the mean annual recruitment during the years immediately before the change in fishing intensity. In this sense, therefore, the above figures show the most likely changes during the years of transition. They can also show the *relative* picture fairly accurately when recruitment is fluctuating, in that they give approximately the transitional yields relative to those that would have been obtained had no change in fishing intensity taken place. For example, if it is possible to detect the presence of a strong year-class before it enters the exploited phase of the population, it might be desirable to make the reduction in fishing intensity coincide with its entry to the exploited phase. This would reduce the initial drop in yield indicated in Figs. 19.10 and 19.11 and may eliminate it altogether if the incoming year-class is particularly abundant, though the catch would still be proportionately less than would have been obtained if no decrease in fishing intensity had been made.

The other complication that needs to be considered is the dependence of parameters on density. The full calculation of transitional yield equations including this dependence is complicated, but it is possible to anticipate what kind of differences would result when such phenomena exist. It can be said, in general, that the difference between predictions based on simple transition equations and those incorporating the density dependence of parameters will be least for the first of the transitional years and greatest when the final steady state is reached. Usually the differences for the first year would be virtually negligible, and as far as the dependence of recruitment on population density is concerned there can be no effect at all until at least $t_{\rho'}$ years have elapsed. Since the yield in the final steady state can be calculated without using transition equations, we can easily estimate the maximum differences, and in Figs. 19.10 and 19.11 the final equilibrium yields calculated using hypothesis (b) of §18.4.1 for the relationship between growth and density in plaice are shown as dotted lines. If there is some dependence of recruitment on density then the actual yield in the final steady-state may be higher than that predicted with constant parameters.

The other important effect introduced by making parameters density dependent is the prolongation of the transitional phase; in fact, the final steady state is not theoretically reached until an infinite time has elapsed. The actual changes will depend on the relative importance of the density dependence of factors such as growth and mortality on the one hand, which will tend to increase the period required before the original steady yield is regained and the initial losses are made up, and recruitment on the other, which will have the opposite effect. However, most of the important changes take place during the first few years of the transitional period, and as we have mentioned above, these are likely to be the least affected by such complications.

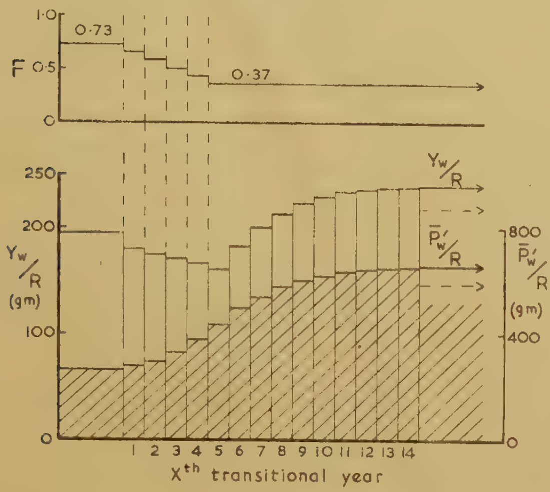

FIG. 19.12 PLAICE: TRANSITIONAL PHASE FOLLOWING A SERIES OF REDUCTIONS IN FISHING INTENSITY

[Yield and catch per unit effort following a reduction in fishing intensity to half the pre-war level in five equal stages at yearly intervals, i.e. a change in *F* from 0·73 to 0·37 in steps of 0·073. Other details as in Fig. 19.10.]

The next question to consider is the extent to which the large initial drop in yield shown in Figs. 19.10 and 19.11 can be avoided by changing the fishing intensity by stages, particularly as a large and sudden decrease in this factor might, for economic reasons, be difficult to achieve in practice. We therefore consider two examples of other possible ways in which the reduction in fishing mortality from 0·73 to 0·37 previously examined might be brought about. In the first, this change is made in equal steps covering a period of five years, the fishing mortality coefficient being decreased by 0.072 each year as shown in the upper diagram of Fig. 19.12. The transitional yields shown in the lower part of this figure are calculated from (8.19). It will be seen that the yield decreases steadily during the period in which the fishing mortality coefficient is decreasing, but never reaches as low a value as in either the first or second year of Fig. 19.11. However, equilibrium is not theoretically reached until a further ten years have elapsed after the fishing mortality coefficient reaches 0·37, though effectively about eleven years after the initial change. Furthermore, the original equilibrium level of yield is not regained until six years have elapsed, and a further five years are required to make up the initial losses.

For the second example we take the same overall decrease in fishing intensity in the same five equal steps, but suppose that a year's respite is allowed between each change so that the yield may partially recover. The resulting transitional yields are shown in Fig. 19.13. It will be seen that they never fall far below the original steady level, but the times taken to reach the new equilibrium, to regain the original level of yield and to recover the initial losses, are all greater than before.

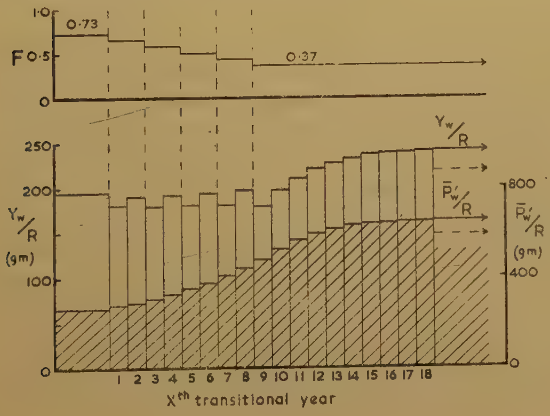

FIG. 19.13 PLAICE: TRANSITIONAL PHASE FOLLOWING A SERIES OF REDUCTIONS IN FISHING INTENSITY

[Yield and catch per unit effort following a reduction in fishing intensity to half the pre-war level in five equal stages at two-yearly intervals. Other details as in Fig. 19.10.]

In both the above examples the catch per unit effort increases throughout the transitional phase, as shown by the shaded histograms, and this is indeed a general characteristic however the reduction in fishing intensity is made. It will be noted that since even in the first transitional year the yield never falls by quite the same proportion as the fishing intensity, the profit margin will gradually increase throughout the transitional phase provided the cost of fishing falls in the same proportion as the fishing intensity. For this to happen would usually require the reduction in fishing intensity to be made by a permanent decrease in the fishing power of the fleet; other methods, such as restriction of fishing time, would not cause the cost of fishing to fall to the same extent, in which case the profit margin may not exceed its previous level until later in the transitional phase.

From the point of view of regulative procedure, better discrimination between the three methods considered above of approximately halving the fishing intensity can be obtained by plotting the differences between the cumulative yields resulting from each type of change and the cumulative yield obtained if no change had been made. These are shown in Fig. 19.14 according to the following key:—

Curve (a) Fishing mortality 0·73 → 0·37 in a single step.
Curve (b) Fishing mortality 0·73 → 0·37 in steps of 0·072 at yearly intervals.
Curve (c) Fishing mortality 0·73 → 0·37 in steps of 0·072 at two-yearly intervals.

It will be seen that although the single-stage reduction results in the greatest initial loss of yield, nevertheless the previous level of yield is regained, and the initial loss made up, sooner than with either of the more gradual reductions.

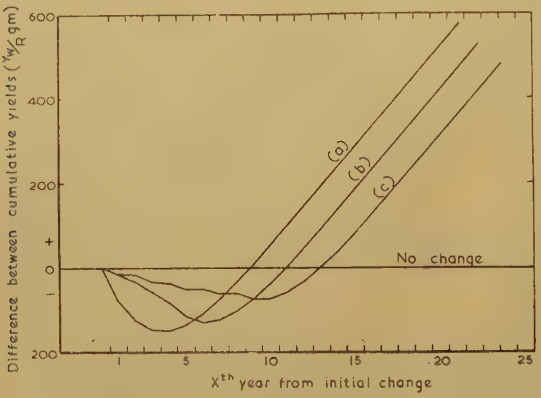

FIG. 19.14 PLAICE: CUMULATIVE YIELDS DURING TRANSITIONAL PHASES

[Differences between cumulative yields following a reduction in fishing intensity to half the pre-war level and that if no reduction had been made: (a) one-stage reduction (Fig. 19.11); (b) five yearly stages (Fig. 19.12); (c) five two-yearly stages (Fig. 19.13).]

Before leaving this discussion of the transitional stages following a change in fishing intensity, it may be of interest from the point of view of the interpretation of the past history of a fishery to consider the consequences of an increase in this factor. We take as our example an increase in F in plaice from 0·55 to 0·73, and the transitional yields are shown in Fig. 19.15. This change in F is opposite to that of Fig. 19.10, and the corresponding changes in yield are similarly the converse of those shown there. Thus the yield, after initially increasing, falls to its original level in the third transitional year, and the initial gains are lost after seven years have elapsed; further, the final level of yield is now lower than the initial. The catch per unit effort now falls throughout the transitional period, instead of increasing as in Fig. 19.10. This shows the effect of an expansion of fleet size on the catch per day's absence or per hour's fishing, but an increase in F might also be brought about by improvements in gear efficiency without any change in fleet size.* For example, an increase in F from 0·55 to 0·73 is roughly that which might have occurred in the plaice fishery following introduction of the Vigneron-Dahl gear, heavier

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*The reader will remember that we defined 'fishing effort' in §3.3 in standardised units of fishing power, so that an increase in gear efficiency will cause a proportional increase in fishing effort but leave fishing time unchanged. Hence the distinction made here between changes in catch per unit effort and changes in catch per unit fishing time.

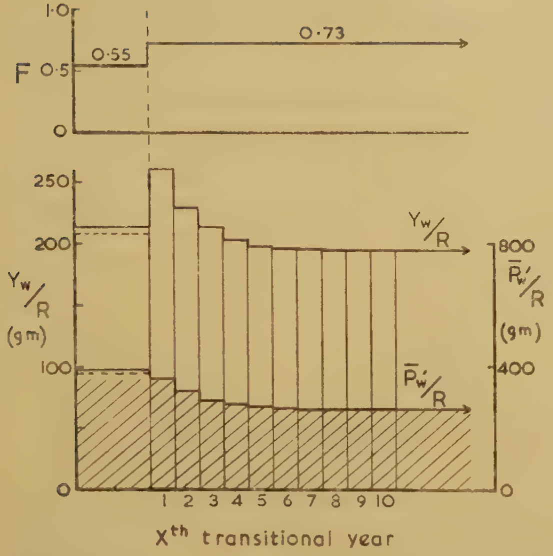

FIG. 19.15 PLAICE: TRANSITIONAL PHASE FOLLOWING AN INCREASE IN FISHING INTENSITY

[Yield (open histogram, left hand scale) and catch per unit effort (shaded histogram, right hand scale) following an increase in fishing intensity from 75% of the pre-war level to the pre-war level, i.e. a sudden increase in F from 0·55 to 0·73. Other details as in Fig. 19.10.]

ground ropes, tickler chains, etc., except that these innovations were spread over several years. In this case the catch per unit *fishing time* changes during the transitional period in the same way as the yield itself—in each a temporary rise is followed by a decrease to a final level lower than the initial. This illustrates very clearly one of the main features to be found in the development of unregulated fisheries, namely that as exploitation has intensified, increases in vessel or gear efficiency have brought only temporary improvements, the fishery soon becoming less profitable than before. A British recommendation at the Overfishing Conference of 1946 referred to in §19.2.1.1 was that, as a first step towards rational exploitation of the North Sea, fishing intensity should be limited to 85% of its pre-war level, and that if subsequent improvements in vessel or gear efficiency took place the total fleet size or the total time spent fishing should be decreased to maintain the same fishing mortality. The example of Fig. 19.15 gives some idea of what might happen if this latter proviso is not made. If, in the example of Fig. 19.15, the fishing mortality coefficient had not been allowed to increase (e.g. by making a reduction in total fishing power or time proportional to the increase in efficiency of the new gears), the yield would have been maintained at its previous level but the catch per unit effort would have risen by some 30%. It should be noted that the transitional changes illustrated in Fig. 19.15 refer to the case in which the initial value of F is already greater than $(F)_{\max}$. If it should be below $(F)_{\max}$, the initial increase in yield would be partly maintained, but the catch per unit effort would still fall throughout the transitional period.

19.2.2.2 *Mesh regulation*

The other kind of transitional phase requiring consideration is that following a change in gear selectivity. The example we give is based on the plaice as before, and we suppose that the cod-end mesh is suddenly increased from 70 to 134 mm. with F constant at 0·73 throughout; from Fig. 15.13 this can be seen to correspond to an increase in the age at first capture from ${}_0t_{\rho'} = 3{\cdot}72$ years to ${}_1t_{\rho'} = 5{\cdot}0$ years, and Fig. 17.8 shows that the final steady yield would be rather greater than that resulting from halving the pre-war fishing intensity. Equations (8.28) and (8.31) of §8.2.2 give the method by which the yield per recruit in each of the transitional years following this change in mesh may be calculated. With the above values of ${}_0t_{\rho'}$ and ${}_1t_{\rho'}$ we find $V = 1$ and $v = 0{\cdot}28$ and since we also have $\alpha = \beta$, the yield in the first of the transitional years is given from (8.28) by

$$ {}_1Y_W = A\sum_{n=0}^{3} B_n\{e^{-\alpha-\delta v}(1-e^{-\alpha(1-v)}) + e^{-2\alpha} - e^{-\alpha\lambda_0}\} $$

For all subsequent transitional years we have from (8.31)

$$_xY_W = A\sum_{n=0}^{3} B_n[e^{-\delta(1+v)}\{1 - e^{-\alpha(X-1-v)} + e^{-\gamma' - \alpha(X-2-v)}(1 - e^{-\alpha})\} +$$
$$+ e^{-\alpha(X+1)} - e^{-\alpha\lambda_0}]$$

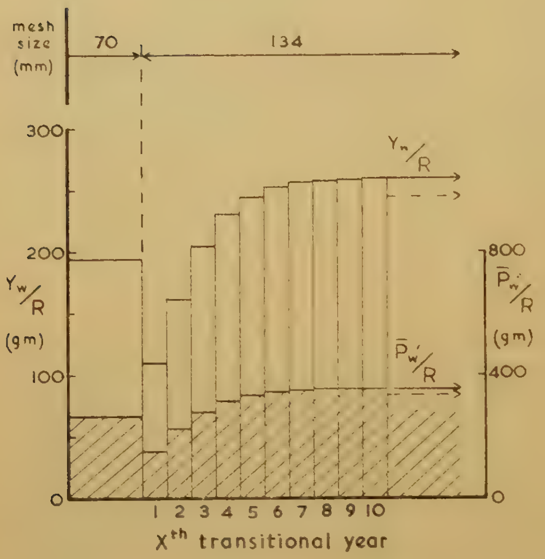

FIG. 19.16 PLAICE: TRANSITIONAL PHASE FOLLOWING AN INCREASE IN MESH

[Yield and catch per unit effort following a sudden increase in mesh from 70 to 134 mm. as shown at the top of the diagram. This increase in mesh is equivalent to a change in $t_{\rho'}$ from 3·72 to 5 yrs. Other details as in Fig. 19.10.]

Figure 19.16 shows the annual yields during the whole transitional period, and it will be seen that although the fall in yield in the first transitional year is slightly greater than that following a sudden decrease in fishing intensity to half its pre-war value (Fig. 19.11), the recovery is decidedly more rapid. With the mesh change the original level of yield is regained during the third transitional year compared with the fifth for the reduction in fishing intensity, while the total loss of yield is made up during the fifth year compared with the ninth. On the other hand, the catch per unit effort following a mesh change remains proportional to the yield itself and therefore falls at first, as shown by the shaded histogram of Fig. 19.16, whereas with a reduction in fishing intensity it increases throughout the transitional period. The effect on these transient yields of a fluctuating recruitment is similar to that discussed in connection with a change in fishing intensity, except that the yield in the first year following an increase in mesh size must always be lower than that in the preceding year if $V \geqslant 1$ year. The effects of dependence of parameters on density are also similar to those for a change in fishing intensity, being least for the first of the transition years and greatest when equilibrium is reached.

Fig. 19.17 shows the transitional changes if the above increase in mesh size is made in two stages, allowing the population to reach stability after the first. The two increases are such that each causes $t_{\rho'}$ to increase by the same amount, i.e. by 0·64 years; from Fig. 15.14 it is seen that the required mesh changes are from 70 to 118 mm. for the first stage and from 118 to 134 mm. for the second. Since V is now zero, the yield during any transitional year is given by (8.29) with $\alpha = \beta$, i.e.

$$_xY_W = A\sum_{n=0}^{3} B_n\{e^{-\delta v}(1 - e^{-\alpha(X-v)}) + e^{-\alpha X} - e^{-\alpha\lambda_0}\}$$

Comparison with Fig. 19.16 shows that although the initial loss of yield following each change is less, as would be expected, it still takes as long to recover the original level of

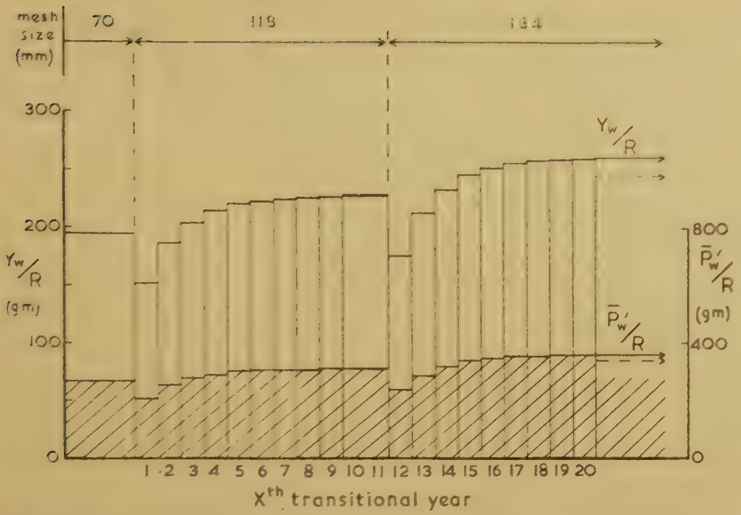

FIG. 19.17 PLAICE: TRANSITIONAL PHASE FOLLOWING TWO INCREASES IN MESH SIZE

[Yield and catch per unit effort following increase in mesh from 70 to 118 mm. followed by a further increase from 118 to 134 mm., as shown at the top of the diagram. Each of these changes is equivalent to an increase in $t_{p'}$ of 0·64 yrs. Other details as in Fig. 19.10.]

yield and to make up the initial losses. This contrasts with the changes following a reduction in fishing intensity, where the smaller is the reduction the more rapidly is the yield regained and the losses made up (cf. Figs. 19.10 and 19.11).

For our final example of transitional changes we consider an increase in mesh size that also causes the efficiency of the gear to increase. It is convenient to use the haddock for illustrating this kind of transition, and we examine the effect of an increase in mesh size from 70 to 80 mm., i.e. from $t_{p'} = 1{\cdot}83$ years to 2·43 years. This value of $v = 0{\cdot}6$ years is nearly the same as that involved in each of the stages illustrated for plaice in Fig. 19.17. In examining the results of the Shields mesh experiment on haddock (§14.2.2) it was found that the number of fish caught by the larger cod-end (83 mm. mesh) above its selection range was about 27% greater than that by the smaller meshed cod-end (70 mm.). If this is taken as an estimate of the actual increase in fishing power, and if it is assumed that intermediate changes in mesh size within this range would cause a proportionate change in fishing power, then for a change from 70 mm. to 80 mm. the increase in fishing power would be about 20%. With the fishing mortality coefficient initially having the value $F_0 = 1{\cdot}0$, that after the mesh change is consequently $F_1 = 1{\cdot}2$. Since in this case $V = 0$, (8.29) can again be used to compute the yield in each transitional year, remembering that α and β are now different.

The histogram drawn with continuous lines in Fig. 19.18 shows the transitional yields computed in this way, while that with broken lines shows for comparison the effect of the same change in mesh but with no increase in gear efficiency, i.e. with $F = 1.0$ throughout. It will be seen that the result of increased gear efficiency in this case is to reduce the initial loss of yield to about half the loss with no change in efficiency, and to cause the losses to be

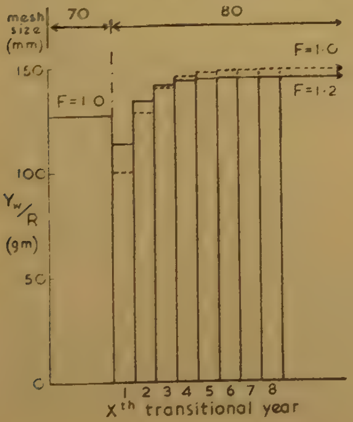

FIG. 19.18 HADDOCK: TRANSITIONAL PHASES FOLLOWING AN INCREASE IN MESH SIZE

[Yield following an increase in mesh from 70 to 80 mm. Broken lines, no change in gear efficiency, $F = 1{\cdot}0$ throughout; continuous lines, gear efficiency increased by mesh change, F increasing from 1·0 to 1·2.]

made up in the third year instead of the fourth, despite the fact that the final steady yield is lower. It is also interesting to compare the histogram for no change in gear efficiency with that of Fig. 19.17 for the plaice. Although the increase in $t_{p'}$ is nearly the same in each case and the yields in the first transitional year are each about 20% lower than the previous level, the transitional changes are more rapid in haddock than plaice. Thus the previous level of yield is regained, and the losses made up, about one year earlier in the haddock.

19.2.3 *Maintenance of a regulated fishery—the use of control charts*

In the preceding sections we have commented on the merits of various methods by which a fishery may be brought to a state of eumetric and optimum fishing, and have demonstrated the behaviour of the fishery to be expected during the transitional period following the introduction of certain regulative measures. Here we touch on some aspects of the final phase of regulation, that of maintaining the fishery in a desired steady state. This process we shall distinguish by the term *fishery maintenance*, since the problems involved are of a kind different from those encountered previously. Thus two important functions of fishery maintenance are to ascertain whether the steady state approached after regulation has been put into effect is within predicted limits, and to analyse the subsequent history of the fishery with a view to detecting the occurrence of any changes that would necessitate revision of the particular regulative measures adopted.

Clearly, these are matters that can be investigated thoroughly only by analytical studies of the changes in population parameters before and after regulation, particularly the magnitude of the fishing mortality coefficient or the age at entry to the exploited phase—depending on whether fishing intensity or gear selectivity is being regulated. Secondary effects such as the possible changes in recruitment and growth with density also need to be investigated. Nevertheless, there is bound to be an attempt to judge the efficacy of regulation merely by the changes in yield or catch per unit effort that are observed; indeed, as far as the fishing industries are concerned, these are, ultimately, the only test. Again, desirable though it may be to continue intensive study of a fishery after regulation, it may be wished to divert research effort to other fisheries. Thus it is of considerable practical importance to find to what extent a knowledge of the annual yield from a regulated fishery, combined with a detailed study of the fishery prior to regulation, can be used to test whether the prescribed regulative measure is having the desired effect.

This raises a number of problems, which will vary in detail from one fishery to another and will depend also on the particular method of regulation adopted. The basic principles, nevertheless, have much in common with those pertaining to the control of an industrial process, and in what follows we offer some preliminary comments on the application of the statistical control chart technique to fishery maintenance. The use of this technique for the analysis of the Columbia River fishery for Chinook salmon has been demonstrated by Rich (1943), while Rounsefell and Bond (1950) have used it to interpret fluctuations in growth of Atlantic salmon; in the present case we are concerned with a somewhat different problem, since we wish to know whether the contemporary behaviour of the fishery is within limits that cannot be established by direct observation but can only be predicted from a study of the fishery prior to regulation. Burkenroad (1951) has stressed the importance of establishing conclusively the effects of regulation, and has suggested that it should be treated as a controlled experiment with alternate imposition and relaxation of regulative measures to provide data which can be examined statistically. Whether this is a practicable procedure for major commercial fisheries is questionable, but Burkenroad's point emphasizes the need to be able to establish as soon as possible from catch and, possibly, effort data whether regulation is having a significant effect. It is clear, however, that something more than the usual statistical techniques will be necessary, because the year-to-year variation of a fishery after regulation will differ from that observed before it, and the expected difference must be assessed before statistical tests can be applied.

It will be realised that the main problem concerns the interpretation of year-to-year fluctuations in a fishery with reference to certain central values which, in the first instance, have to be predicted. Although such fluctuations are largely irrelevant, or at most of secondary interest, in a general discussion of rational fishing and regulation, they assume great importance when it comes to making the prediction necessary for an adequate test of the efficacy of regulation. The most important factor here, and the one on which much earlier research concentrated, is the fluctuation in recruitment and its effect on the annual yield. Some progress in the theoretical treatment of this has been made and applied in §15.2.2 to obtain a rough appreciation of the sampling error of age-composition data, and the same methods can be used as a starting point in the analysis of the present problem.

We take as our example a fishery in which the fishing intensity has increased to a point at which the stock is over-fished and has then remained at a roughly constant level for some years. This will be recognised as the course of events in the North Sea plaice and haddock fisheries and is likely to be fairly typical. We then suppose that regulation is introduced, by means of reduction of fishing intensity or increase of mesh size or both, and that after the transitional phase is over a new steady state is established with the population fluctuating about a new mean level of abundance as the result, primarily, of fluctuations in recruitment. It is not necessary to assume that the fishing intensity is exactly constant before and after regulation, provided its variation is not large and makes roughly the same proportional contribution to the variation of yield in both periods. If these conditions did not hold, as might be the case if the fishery were regulated for example by means of catch quotas, it would be necessary to develop an expression for the variance of yield which takes specific account of the variation of fishing intensity as well as that of recruitment.

Let us suppose that a particular combination of fishing intensity and mesh size is specified as a regulative measure, and that by means of the appropriate population model the resulting mean level of yield when the new steady state is reached is predicted as ${}_p\bar{Y}_W$. One form of control chart could therefore be constructed from this predicted mean yield with upper and lower confidence limits based on some appropriate multiple of the predicted standard deviation of the annual yield. Each annual yield after the new steady state had been reached would be entered on this chart, and if a value lay outside the limits it could be presumed that some significant change in the fishery had occurred.

The above kind of control chart, in which each annual yield is entered independently, will be of value in detecting a sudden departure from the predicted behaviour, but will be limited by the fact that the effect on the yield of a particularly high or low recruitment will extend over several years, because annual yields are serially dependent (see §15.2.2). A control chart of this kind must therefore be interpreted with care, and the fact that a succession of annual yields lay above or below the mean would not necessarily indicate that any significant change had occurred—as it would if each yield were an independent quantity. The detection of long-term trends and systematic variation might indeed be better accomplished with a control chart on which are entered successive values of the mean yield, $\bar{Y}_W$. Each value would be the mean of all the annual yields from the attainment of the steady state to the present time, and they would be expected to approach the predicted value as the duration of the steady state increased. The sensitivity of such a control chart for detecting a permanent departure from the expected state would therefore, unlike one for annual yield, increase with time, since each year's entry would, in effect, summarise the history of the fishery over the whole of the maintenance phase. A further advantage of using mean yield is that it is a quantity whose distribution is likely to be closely normal, even though that of the annual yield may depart somewhat from normality. The confidence limits for a control chart for mean yield must, nevertheless, take into account the fact that successive values of $\bar{Y}_W$ will be based on an increasing number, q, of annual yields that are serially dependent. We therefore require an expression for the variance of mean yield as a function of the number of individual yields from which it is computed, that takes serial dependence into account.

Let us suppose that the steady state is effectively reached in the year X and that we compute a mean yield starting from this year. Although the individual annual yields will not be independent, each will be made up of year-classes which, to a first approximation, can be regarded as independent*, and we therefore need to express mean yield as a function of q in terms of the year-classes involved. We are grateful to our colleague Mr. J. A. Gulland for assistance with this problem and for pointing out to us that the treatment can be developed from that given in §6.2 for obtaining (6.30) for $\bar{Y}_W$. Two cases must be distinguished: (i) in which $q \leqslant \lambda$, and (ii) in which $q > \lambda$.

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*Strictly, successive recruit values are themselves auto-correlated (unless recruitment is near an asymptotic limit) but usually to a much less degree than successive annual yields.

For case (i), we can group into three categories the year-classes present in one or more of the annual yields in q years: (a) those that are present in each annual yield throughout the period, (b) those that entered the exploited phase of the population prior to year X and which reach age t_λ before year $X - q$, and (c) those that enter the exploited phase after year X but before year $X - q$. The mean yield over q years from year-classes of category (a) can be expressed by the methods of §6.2 in the form

$$({}_a\bar{Y}_W)_q = \frac{1}{q}\sum_{p=0}^{\lambda-q} {}_{X-p}R \sum_{\theta=p+1}^{p+q} u_\theta$$

The mean yield from year-classes of category (b) is

$$({}_b\bar{Y}_W)_q = \frac{1}{q}\sum_{p=1}^{q-1} {}_{X-\lambda+p}R \sum_{\theta=\lambda-p+1}^{\lambda} u_\theta$$

while that from category (c) is

$$({}_c\bar{Y}_W)_q = \frac{1}{q}\sum_{p=1}^{q-1} {}_{X+p}R \sum_{\theta=1}^{q-p} u_\theta$$

It will be noted that no one year-class is present in more than one category, and hence all of the above expressions are independent. Thus we predict the variance of the total mean yield, $({}_p\sigma^2_{\bar{Y}})_q$, by summing the component variances and putting the variance of R in every category equal to σ^2_R. So we find

$$({}_p\sigma^2_{\bar{Y}})_q = \frac{\sigma^2_R}{q^2}\left[\sum_{p=0}^{\lambda-q}\left(\sum_{\theta=p+1}^{p+q} u_\theta\right)^2 + \sum_{p=1}^{q-1}\left\{\left(\sum_{\theta=\lambda-p+1}^{\lambda} u_\theta\right)^2 + \left(\sum_{\theta=1}^{q-p} u_\theta\right)^2\right\}\right] \quad \ldots \quad (19.1)$$

which is the required expression.

For case (ii), with $q > \lambda$, we again group the year-classes into three categories analogous with those above. Thus category (a) consists of those year-classes that are present throughout their fishable life-span during the period q years, category (b) consists of those that entered the exploited phase prior to year X, while category (c) consists of year-classes that enter the exploited phase between year $X - q - \lambda - 1$ and year $X - q$, and hence do not complete their life-span during the period. By the same methods we find

$$({}_a\bar{Y}_W)_q = \frac{1}{q}\sum_{p=0}^{q-\lambda} {}_{X-p}R \sum_{\theta=1}^{\lambda} u_\theta$$

$$({}_b\bar{Y}_W)_q = \frac{1}{q}\sum_{p=1}^{\lambda-1} {}_{X-p}R \sum_{\theta=p+1}^{\lambda} u_\theta$$

$$({}_c\bar{Y}_W)_q = \frac{1}{q}\sum_{p=1}^{\lambda-1} {}_{X-q-p}R \sum_{\theta=1}^{p} u_\theta$$

Again, these expressions are independent, and we have

$$({}_p\sigma^2{}_{\bar{Y}})_q = \frac{\sigma^2{}_R}{q^2}\left[\left(\sum_{\theta=1}^{\lambda} u_\theta\right)^2 (q - \lambda + 1) + \sum_{p=1}^{\lambda-1}\left\{\left(\sum_{\theta=p+1}^{\lambda} u_\theta\right)^2 + \left(\sum_{\theta=1}^{p} u_\theta\right)^2\right\}\right] \quad .. \text{ (19.2)}$$

It will be noted that when $q = 1$, (19.1) reduces to

$$({}_p\sigma^2{}_{\bar{Y}})_1 = \sigma^2{}_R \sum_{\theta=1}^{\lambda} u^2{}_\theta$$

which is identical with (6.31), and as $q \to \infty$ we find from (19.2) that

$$({}_p\sigma^2{}_{\bar{Y}})_q \to \frac{\sigma^2{}_R}{q}\left(\sum_{\theta=1}^{\lambda} u_\theta\right)^2 = \frac{\sigma^2{}_R}{q}\left(\frac{\bar{Y}_W}{R}\right)$$

The form of the control charts for yield and mean yield based on the above theory can be demonstrated by an example based on the North Sea plaice fishery, for which the necessary data have been given in §15.2.2. There we found that the observational error variance of the recruit estimates was

$$\sigma_e{}^2{}_{R_X} = 0{\cdot}23 \times 10^{16}$$

Hence our best estimate of the true recruit variance during the pre-war steady state is

$$\sigma^2{}_{R_X} = (1{\cdot}08 - 0{\cdot}23) \times 10^{16} = 0{\cdot}85 \times 10^{16}$$

For purpose of illustration we suppose that a regulative measure is prescribed such that, if properly enforced, it would be expected to reduce the fishing mortality coefficient to half its pre-war value, i.e. to $F = 0{\cdot}37$. Using constant parameters gives the predicted mean European yield of plaice in these circumstances as

$${}_p\bar{Y}_W = 13 \times 10^5 \text{ cwts.}$$

while the predicted standard deviation of annual yield is

$${}_p\sigma_Y = 1{\cdot}6 \times 10^5 \text{ cwts.}$$

Taking plus and minus twice the standard deviation for upper and lower confidence limits approximating to the 0·05 significance level*, gives the control chart shown in Fig. 19.19, where the predicted mean yield is indicated by the horizontal line (— — —) and the confidence limits for annual yield by the continuous horizontal lines. Confidence limits for mean yield covering a period of thirty years after the steady state has been reached are calculated from (19.1) for the first eleven years and from (19.2) thereafter (since $\lambda = 11$ years); these are shown by the curved lines of Fig. 19.19. For comparison, the mean yield before regulation is shown in the figure by a horizontal line (— · — ·); it will be noted that although this initially lies within the lower confidence limits for both annual yield and mean yield, it is outside that for mean yield after about eight years.

The validity of control charts for Y_W and $\bar{Y}_W$ such as these depends, *inter alia*, on there being adequate agreement between the actual and predicted *variance* of annual yield.

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*Since the control chart is in this case based on estimates derived from only nine observations (years 1929-37), confidence limits imply a little lower level of significance than is usual for the multiple of the standard deviation adopted. However, the question of deciding what level of significance is to be interpreted as showing that the process has 'gone out of control' is, in any case, arbitrary, and it would be erring on the safe side to have limits that tended to be a little narrower than they should for the level of significance desired.

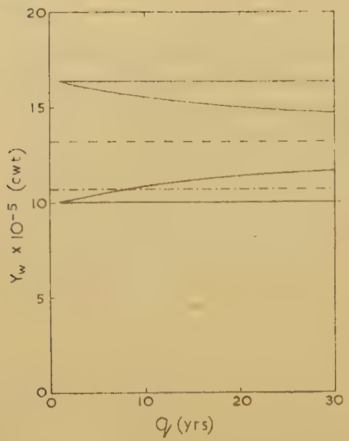

FIG. 19.19 PLAICE: CONTROL CHARTS FOR ANNUAL YIELD AND MEAN YIELD

[Fishing intensity is taken to be reduced from its pre-war level to half this amount by regulation. The original mean level of yield is shown as –·–·–, that after the new steady state is reached as – – – – Horizontal lines are confidence limits for annual yield after regulation, curved lines are confidence limits for mean yield calculated from the year in which the new steady state is reached (the origin of the time scale).]

In addition, it would therefore be desirable to construct a control chart for σ^2_Y in order to detect a significant departure in this quantity which might necessitate a revision of the confidence limits of the control charts for Y_W and $\bar{Y}_W$. Owing to the serial dependence of annual yields the observed variance of yield will increase as q increases, but this increase can be computed from (15.13). To establish the control limits for variance it would be necessary to develop an expression for the variance of the variance of yield, taking serial dependence into account.

To conclude this discussion of the application of the statistical control chart technique to fishery management, we should mention a few points concerning the interpretation of charts for Y_W and $\bar{Y}_W$ such as are shown in Fig. 19.19. When this technique is used for the control of an industrial process the characteristics analysed in this way are usually some direct measure of the physical properties of a product, such as its dimensions. Consequently, when a control chart indicates that one of these characteristics has 'gone out of control' the cause is usually apparent or, at least, can be fairly easily localised to a particular operation. With control charts of the kind suggested above, the observation that the yield in a certain year, or the mean yield up to that year, lies outside the confidence limits will never be sufficient in itself to indicate the cause.

With regulation of effort, probably the first step would be to see whether the fishing mortality coefficient has a value reasonably near to that expected, since even though reliable effort statistics may be available to show that the prescribed change in fishing effort has in fact been carried out, there is always the possibility that some undetected change in searching power or gear efficiency may have altered the relationship between fishing intensity and the fishing mortality coefficient. Similarly, with a mesh regulation, it would be necessary to measure the change in the incidence of fishing mortality in those age-groups within the selection ranges of the old and new meshes, as well as its magnitude in the exploited phase to test whether the change in mesh could have altered the efficiency of the gear. If nothing abnormal is brought to light by these observations, then it would be presumed that a change in some property of the population was responsible for the yield 'going out of control'. For example, the relationship between density and growth might have been incorrectly assessed, which would result in the predicted values of the weighting coefficients u_θ being in error; or a change in recruitment might have been brought about by the changed egg-production or by a sustained environmental change external to the population affecting the larval mortality coefficients. To trace factors such as these it would be necessary to undertake further research on the dynamics of the population, perhaps as detailed as that during the pre-regulation phase on which the control chart is based. Apart from detecting the cause of the process going out of control, this investigation would probably be required to revise the regulation of the fishery in the light of the changes that had taken place.

The above type of control chart for yield and mean yield is probably the simplest that can be devised and makes use of the minimum of data, though we would stress again that a more detailed statistical study of variation in recruitment and the effect of serial dependence on quantities such as the variance of the variance of the annual yield would be worthwhile. Given more information, other types of control charts could be devised having greater sensitivity, particularly for the detection of significant changes in annual yield. Thus if reliable effort statistics were available it would be possible to estimate the contemporary stock abundance and hence to predict future yields with closer confidence limits; it would also enable control charts of catch per unit effort to be constructed, permitting the contribution of effort variation to the variance of yield to be taken into account. The control process could be refined still further if some measure of the contemporary *structure* of the population were available, preferably the age-composition, although length-composition would be useful. Ultimately, the process would reduce to one of setting up control charts for each of the major factors, mortality, growth and, particularly, recruitment. Some aspects of the problem of predicting recruitment have been discussed in §15.2.3.2. Here we need do no more than note that unless the whole range of egg-production is so high that all recruitments are effectively at an asymptotic limit, successive recruit values form an auto-correlated time series owing to their dependence on egg-production which, in turn, depends on previous values of the recruit series. This makes a rigorous statistical treatment of recruit prediction difficult, although powerful methods, based on a synthesis of the statistical theory of auto-correlation and certain concepts of communication engineering, have recently been developed for predicting the most probable future of a time series (Wiener, 1949; Westcott, 1950), and appear to be applicable to such problems of fishery control.

From these remarks it is clear that the construction and interpretation of control charts for fishery maintenance is not as straightforward as in the control of a manufacturing process. We regard their main function as one of condensing what is known about a fishery before regulation in a form that enables its behaviour after regulation to be compared in an objective and simple way with what would be expected. As such, we suggest they would be indispensable to the proper maintenance of a regulated fishery, especially where detailed investigations cannot be continued indefinitely. An important point emerging from the above investigation is that the construction of control charts for fishery maintenance is not a purely statistical problem, but requires also an understanding of fishery dynamics and the use of theoretical population models to estimate quantities such as the mean and variance of yield after regulation has been introduced.

19.3 Heterogeneous Fishing: The Regulation of an International Fishery

In our discussion of the aims and methods of fishery regulation we have hitherto been concerned primarily with the problem of adjusting the characteristics of the total fishing activity to achieve optimum fishing. Now as we have mentioned previously, one of the characteristics of the North Sea as an exploited area is that fishing is carried out by a number of fleets of different nationalities and of varying sizes, not all of which are using gear with the same selective properties. In this section we see to what extent the conclusions previously drawn are likely to be modified when we have to deal with heterogeneous fishing activity of this kind. In §19.3.1 we discuss the problems involved in an uncoordinated fishery where it is necessary to assess the effect on the yield to one particular fleet of changes in the fishing activity of the remaining fleets, and to find under what conditions attempts at regulation on the part of one fleet only can be beneficial. The methods developed for these purposes serve as a basis for a discussion in §19.3.2 of some of the problems that arise in the regulation of an international fishery.

19.3.1 *Partition of yield between two fleets operating independently*

We first state one principle which is fundamental to the analysis of situations involving heterogeneous fishing activity, and which first arose in §8.1.3. This is that if two or more fleets are using gear having the same selective properties the fishing mortality coefficients generated by each are additive, but if their gears are of differing selectivities then each fleet must be dealt with separately. The corollary of this is that the catches of each of a number of fleets, provided they are all using gear with the same selectivity, are proportional to the fishing intensities exerted by each. This statement holds good for that particular group of fleets even though there may be other fleets exploiting the same population that are using gear with differing selectivity. In the following discussion we therefore need to distinguish between cases in which fleets differ only because they generate different fishing intensities, and those in which fleets differ also because they are using gear with differing selective properties. It will be appreciated that the effect of changes in the fishing intensity or gear selectivity of one or more fleets depends on the particular balance between these characteristics that existed in the steady state prior to those changes, and this fact will need to be taken into account in the following examples.

19.3.1.1 *Gear selectivities the same, one fleet changing its fishing intensity*

For our first example we consider two fleets, A and B, exerting fishing mortality coefficients ${}_AF$ and ${}_BF$ respectively, but using the same cod-end mesh. We base this example on plaice, and use simple population models with $t_\rho = t_{\rho'} = 3{\cdot}72$ years to refer to both fleets; that is, we shall suppose that both fleets are fishing the same population, using a 70 mm. mesh and are distributed similarly over it.

In the first instance we suppose that the initial fishing mortality coefficients generated by each fleet, denoted by ${}_AF_0$ and ${}_BF_0$ and corresponding to fishing intensities ${}_Af_0$ and ${}_Bf_0$, together give a total mortality coefficient of $0{\cdot}73$. If one fleet, say fleet A, changes its fishing intensity to some specified value, say ${}_Af$, we wish to see what the effect would be on its own yield, on that of fleet B, and on the total yield from the population. With the same mesh in use by both fleets the calculation is simple, since from (8.15) we have

$$\frac{{}_AY_W}{R} = \frac{{}_Af}{{}_Af - {}_Bf_0}\left(\frac{Y_W}{R}\right)$$

and

$$\frac{{}_BY_W}{R} = \frac{{}_Bf_0}{{}_Af + {}_Bf_0}\left(\frac{Y_W}{R}\right)$$

where ${}_AY_W/R$ and ${}_BY_W/R$ are the yields per recruit obtained by fleets A and B respectively, and Y_W/R is the total yield per recruit from the population, given by (4.4) with $F = {}_AF + {}_BF_0$.

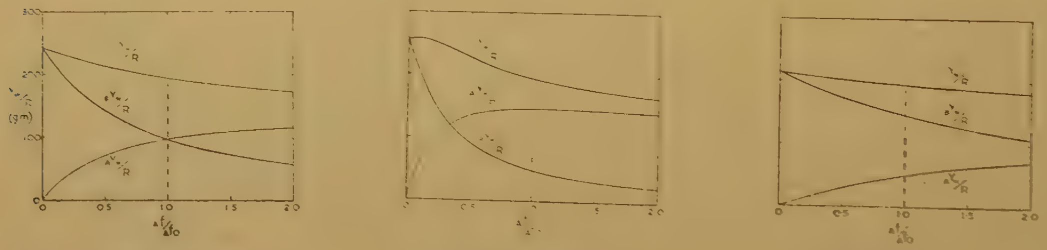

Fig. 19.20.1

Fig. 19.20.2

Fig. 19.20.3

FIGS. 19.20 PLAICE: PARTITION OF YIELD BETWEEN TWO FLEETS OF VARIOUS SIZES

[Examples showing the partition of yield between two fleets exploiting the same phase of the population and using gear of the same selectivity. Fleet A is taken as changing its fishing intensity, with fleet B remaining constant. The abscissae show the change in fishing intensity of fleet A relative to its initial value (vertical line at $Af/Af_0 = (1.0)$. ${}_AY_W/R$ = yield per recruit to fleet A, ${}_BY_W/R$ = yield per recruit to fleet B, Y_W/R = total yield. Three cases are considered, depending on the initial fishing intensities of the two fleets.]

Fig. 19.20.1 Initial fishing mortality coefficients ${}_AF_0 = {}_BF_0 = 0{\cdot}365$.

Fig. 19.20.2 Initial fishing mortality coefficients ${}_AF_0 = 0{\cdot}548$, ${}_BF_0 = 0{\cdot}183$.

Fig. 19.20.3 Initial fishing mortality coefficients ${}_AF_0 = 0{\cdot}183$, ${}_BF_0 = 0.548$.

In Figs. 19.20 are plotted ${}_AY_W/R$, ${}_BY_W/R$, and Y_W/R, as functions of the proportional change in the fishing intensity of fleet A from its initial value, i.e. the ratio ${}_Af/{}_Af_0$, for three different ratios of the initial fishing intensities of the two fleets, viz.:

$$\frac{{}_Af_0}{{}_Bf_0} = 1 \;;\; ({}_AF_0 = {}_BF_0 = 0{\cdot}365) \quad .. \quad .. \quad .. \quad \text{(Fig. 19.20.1)}$$

$$\frac{{}_Af_0}{{}_Bf_0} = 3 \;;\; ({}_AF_0 = 0{\cdot}548,\ {}_BF_0 = 0{\cdot}183) \quad .. \quad .. \quad \text{(Fig. 19.20.2)}$$

and

$$\frac{{}_Af_0}{{}_Bf_0} = 0.33 \;;\; ({}_AF_0 = 0{\cdot}183,\ {}_BF_0 = 0{\cdot}548) \quad .. \quad \text{(Fig. 19.20.3)}$$

In each case a *decrease* in the fishing intensity of fleet A from its initial value results in a decrease in the yield to that fleet, an increase in the yield to fleet B, and an increase in the total yield. The magnitude of the decrease in yield to fleet A depends on the proportion of the initial total fishing intensity contributed by that fleet. Thus, in Fig. 19.20.2, with ${}_AF_0$ constituting three-quarters of the initial total mortality of 0·73, small decreases in ${}_Af$ cause only a very slight drop in ${}_AY_W/R$, and if we had taken ${}_AF_0$ a larger proportion still of the initial total mortality, ${}_AY_W/R$ would have increased to a small extent before declining. *Increases* in the fishing intensity of fleet A, on the other hand, may result in an increased yield to that fleet if ${}_AF_0$ is not too great a proportion of the initial total mortality, (Figs. 19.20.1 and 19.20.3), though when ${}_AF_0/{}_BF_0$ is large, as in Fig. 19.20.2, ${}_AY_W/R$ may fall. The yield to fleet B, and the total yield, both decrease as the fishing intensity of fleet A increases. We must therefore conclude that, in general, an attempt on the part of fleet A to regulate by decreasing its fishing intensity will result in an increased total yield from the population, but unless fleet A is very much larger than fleet B it will be the latter, non-regulating, fleet that obtains the benefit in terms of annual yield. The catch per unit effort of both fleets always increases, however, and that of the regulating fleet more so than that of the non-regulating fleet.

The use of more complex population models for an analysis of this problem is not likely to alter these conclusions greatly, though if the curve of total yield as a function of total fishing mortality is flatter than that given by the simple population models, then fleet A would have to provide an even greater proportion of the total initial fishing intensity before any reduction in its fishing intensity would increase the yield to it. These conclusions depend, however, on whether the value of the initial total mortality ${}_AF_0 + {}_BF_0$ is greater or less than $(F)_{\max}$. In the above examples it is greater, but if it had been less, then of course any decrease in the fishing intensity of fleet A would have decreased ${}_AY_W/R$, and any increase would have increased ${}_AY_W/R$, up to the point at which $({}_AF_0 + {}_BF_0) = (F)_{\max}$.

It will be noted that the same methods can be used to investigate changes in the yield of one particular fleet in competition with any number of other fleets, providing all are using gear having the same selectivity. In this case fleet B of the above examples is to be identified with the whole of the remaining fleets, and the above conclusions remain unchanged.

19.3.1.2 *Fishing intensities constant, one fleet changing its gear selectivity*

The next point to be considered is whether any different picture would be obtained if fleet A had increased the size of its mesh instead of decreasing its fishing intensity, and in this case the yield from each fleet is given by (8.13) and (8.14), which in the case of two fleets with ${}_At_{\rho'} > {}_Bt_{\rho'}$, become

$$\frac{{}_AY_W}{R} = {}_AFW_\infty e^{-M({}_At_{\rho'} - t_\rho) - {}_BF({}_At_{\rho'} - {}_Bt_{\rho'})} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_At_{\rho'} - t_0)}}{{}_AF + {}_BF + M + nK} \left(1 - e^{-({}_AF + {}_BF + M + nK)(t_\lambda - {}_At_{\rho'})}\right) \quad .. \quad .. \quad (19.3)$$

$$\frac{{}_BY_W}{R} = {}_BFW_\infty e^{-M({}_Bt_{\rho'}-t_\rho)}\left\{\sum_{n=0}^{3}\frac{\Omega_n e^{-nK({}_Bt_{\rho'}-t_0)}}{{}_BF+M+nK}\left(1-e^{-({}_BF+M+nK)({}_At_{\rho'}-{}_Bt_{\rho'})}\right)+\right.$$
$$\left.+\,e^{-({}_BF+M)({}_At_{\rho'}-{}_Bt_{\rho'})}\sum_{n=0}^{3}\frac{\Omega_n e^{-nK({}_At_{\rho'}-t_0)}}{{}_AF+{}_BF+M+nK}\left(1-e^{-({}_AF+{}_BF+M+nK)(t_\lambda-{}_At_{\rho'})}\right)\right\} \quad \ldots \quad (19.4)$$

We again take a total fishing mortality coefficient of 0·73, sub-divided between the two fleets in the same three ratios as before, only now the values of ${}_AF$, ${}_BF$ and ${}_Bt_{\rho'}$ remain constant, the latter being equal to 3·72 years, while ${}_At_{\rho'}$ is increased from 3·72 years to 6 years. The behaviour of ${}_AY_W/R$, ${}_BY_W/R$, and the total yield Y_W/R, is shown in Figs. 19.21.

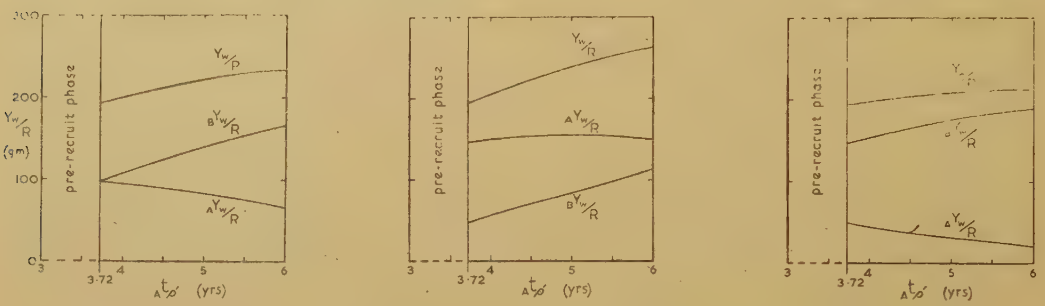

Fig. 19.21.1 Fig. 19.21.2 Fig. 19.21.3

FIGS. 19.21 PLAICE: PARTITION OF YIELD BETWEEN TWO FLEETS USING GEAR OF DIFFERENT SELECTIVITIES

[Fleet A is taken as changing its gear selectivity, the abscissae being the scale of ${}_At_{\rho'}$. The selectivity of the gear used by fleet B remains constant at the value ${}_Bt_{\rho'} = 3·72$ yrs. Fishing intensities of both fleets remain constant, in the ratios defined in the individual diagrams.]

Fig. 19.21.1 Fishing mortality coefficients ${}_AF = {}_BF = 0·365$, ${}_Af/{}_Bf = 1$.

Fig. 19.21.2 Fishing mortality coefficients ${}_AF = 0·548$, ${}_BF = 0·183$, ${}_Af/{}_Bf = 3$.

Fig. 19.21.3 Fishing mortality coefficients ${}_AF = 0·183$, ${}_BF = 0·548$, ${}_Af/{}_Bf = 0·33$.

The general effect of an increase in the mesh size of fleet A is seen to be comparable to a decrease in its fishing intensity, in that only when fleet A is much larger than fleet B does an increase in the former's mesh size result in any increase in its yield (Fig. 19.21.2). In each case the total yield increases and so does that obtained by fleet B. Unlike the effect of unilateral regulation by means of a decrease in fishing intensity, however, the catch per unit effort of the regulating fleet now changes in the same direction as that of the catch itself, and so will increase only when the regulating fleet comprises the greater part of the total effort.

If a number of fleets are concerned, some of which are prepared to make the same change in their mesh size while the remainder make no change, then the same conclusions apply, since ${}_AY_W/R$ will now refer to the total yield obtained by the fleets making the change in mesh, and ${}_BY_W/R$ to the total yield obtained by the remaining fleets. Within each group of fleets the yield to each individual fleet is calculated by sub-dividing ${}_AY_W/R$, or ${}_BY_W/R$ as the case may be, according to the contribution of that particular fleet to the total fishing intensity f_A or f_B, respectively. For every different mesh in use however, we must derive an additional equation, from (8.13) and (8.14), to give the yield obtained by the fleet or fleets which are using it.

19.3.1.3 *Gear selectivities different, one fleet changing its fishing intensity*

In the first example of this section we considered the effect of a reduction in fishing intensity by one of two fleets both of which were using the same mesh. We now see whether any different conclusions would have been reached if the two fleets had been using different meshes. This situation can be analysed by means of (19.3) and (19.4) as before, and we assume that fleet B is using a larger mesh than fleet A, these being specified by the values:

$$_At_{\rho'} = 3{\cdot}72 \text{ years}$$

$$\text{and } _Bt_{\rho'} = 5{\cdot}0 \text{ years}$$

In Table 19.1 are shown values of $_AY_W/R$, $_BY_W/R$, and Y_W/R for various values of $_AF$ (reading horizontally) and $_BF$ (reading vertically). On the basis of this table the following conclusions can be drawn:

(i) The higher the fishing intensity of fleet B, the higher the fishing intensity fleet A has to use in order to get its maximum yield, and vice-versa.

(ii) Any attempt by either fleet to increase its yield by increasing its fishing intensity results in a decrease in the yield to the other fleet.

(iii) Any attempt by either fleet to increase its yield by decreasing its fishing intensity, (i.e. it is initially using a fishing intensity greater than that required to obtain its maximum yield), increases the yield to the other fleet.

(iv) In case (iii) the total yield is also increased, but whether this will happen in case (ii) depends on the particular values of $_AF$ and $_BF$ that are operative.

We may illustrate these conclusions by taking a specific example. Suppose a total fishing mortality coefficient of 0·7 is made up of $_AF = 0{\cdot}6$ and $_BF = 0{\cdot}1$, and we wish to know whether it would benefit fleet A to reduce its fishing intensity even though fleet B was not prepared to make any change. From Table 19.1, for $_AF = 0{\cdot}6$ and $_BF = 0{\cdot}1$, we find:

$$\frac{_AY_W}{R} = 187 \text{ gm.} \;;\quad \frac{_BY_W}{R} = 17 \text{ gm.} \;;\quad \frac{Y_W}{R} = 205 \text{ gm.}$$

this being the initial distribution of yield between the two fleets. If, now, fleet A reduces its fishing intensity to half, i.e. generates a coefficient $_AF = 0{\cdot}3$, then we find:

$$\frac{_AY_W}{R} = 198 \text{ gm.} \;;\quad \frac{_BY_W}{R} = 50 \text{ gm.} \;;\quad \frac{Y_W}{R} = 248 \text{ gm.}$$

Fleet A has therefore gained a small increase in yield, though the yield to fleet B has increased by nearly three-fold, and the total yield has increased. However, the catch per unit effort of fleet A has more than doubled in the process, and it is possible that in these circumstances it would be decided that this decrease in size of fleet A would be beneficial. If fleet A were further reduced, say to one-sixth of its original size (i.e. to $_AF = 0{\cdot}1$) so that each fleet now contributed half the total intensity, we find:

$$\frac{_AY_W}{R} = 145 \text{ gm.} \;;\quad \frac{_BY_W}{R} = 126 \text{ gm.} \;;\quad \frac{Y_W}{R} = 271 \text{ gm.}$$

Although the total yield, and particularly the yield to fleet B, has further increased, the yield to fleet A has fallen. However, since fleet A is now one-sixth its original size, its catch per unit effort is nearly five times as great as it was originally. Whether this further decrease in the size of fleet A was desirable could not be assessed except in terms of economic factors, as discussed in §19.1; it might be, for example, that only by decreasing in size to this extent could fleet A achieve optimum fishing.

Our general conclusion concerning competitive exploitation, by two or more fleets, of the same phase of a population is therefore that only when a particular fleet, or group of fleets, exerts the greater part of the total fishing intensity is an attempt at regulation by it likely to result in its obtaining an increased yield, whether this regulation is carried out by a decrease in fishing intensity or an increase in mesh size. On the other hand, the catch per unit effort of the regulating fleet always increases if regulation takes the form of a reduction in fishing intensity, but with regulation by an increase in the size of mesh it will do so only when the catch itself increases, i.e. when the regulating fleet exerts the greater part of the total intensity. These findings are important because they show the limitations of unilateral regulation where more than one fleet is exploiting an overfished stock.

19.3.1.4 *Two fleets exploiting different phases of the same population*

The examples of heterogeneous activity that we have discussed above are all based on the assumption that the fleets are distributed in the same way with respect to the fish population, or in other words are completely mixed. Some modification of the conclusions would be required if the fleets tended to keep separate and concentrated their activity on different parts of the population, since in such cases the reciprocal effects of changes in the fishing activity of one or more fleets would depend on the rate of interchange of fish between the areas worked by each fleet. Strictly speaking, cases in which the activity of the various fleets is restricted to different parts of the area are more appropriately considered under the heading of spatial variations in fishing activity, because in general they need to be analysed by the methods developed in §10.2 that take the reciprocal interchange of fish into account. We have not made any assessments of this kind for the present paper, but there is a special case which is important and which can be dealt with more simply, namely that of two fleets each exploiting a different phase of the life-history. An example of this is furnished by the North Sea plaice, where the young fish are found mainly on the nursery grounds in the eastern part of the area. Here, although some adult fish are found on the nursery grounds their numbers are a small proportion only of the total adult population. The off-shore dispersion can therefore be treated for the present purpose as a one-way movement only, and we can also use the simplifying assumption that the recruitment migration is knife-edge, all fish entering the main exploited area when they reach age $t_\rho = 3{\cdot}72$ years.

It will be realised that in this sense it is the behaviour of the fish that is rendering heterogeneous the fishing activity of the two fleets, since although the latter may be using gear of the same selective properties, the fleet fishing the older phase cannot catch fish younger than the age at which they migrate from the one area to the other. If we suppose that fleet B is exploiting the adult phase with a 70 mm. mesh, then we can put ${}_Bt_{\rho'} = 3{\cdot}72$ years for that fleet. If fleet A is exploiting the younger phase with the same sized mesh, the value of ${}_At_{\rho'}$ will be about 2 years and we must redefine the recruitment R to the population as a whole as the number of fish that reach this age each year. For the example we suppose that the values of the growth parameters K and W_∞, and the natural mortality coefficient M, are the same for both phases of the population*, the yield obtained by fleet A is then given by

$$\frac{{}_AY_W}{R} = {}_AFW_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_At_{\rho'} - t_0)}}{{}_AF + M + nK} \left(1 - e^{-({}_AF + M + nK)({}_Bt_{\rho'} - {}_At_{\rho'})}\right) \quad .. \qquad (19.5)$$

and that from fleet B by

$$\frac{{}_BY_W}{R} = {}_BFW_\infty e^{-({}_AF + M)({}_Bt_{\rho'} - {}_At_{\rho'})} \sum_{n=0}^{3} \frac{\Omega_n e^{-nK({}_Bt_{\rho'} - t_0)}}{{}_BF + M + nK} \left(1 - e^{-({}_BF + M + nK)(t_\lambda - {}_Bt_{\rho'})}\right)$$

$$.. \qquad .. \qquad (19.6)$$

In Table 19.2 are given values of ${}_AY_W/R$, ${}_BY_W/R$ and the total yield Y_W/R obtained by both fleets, for various values of ${}_AF$ and ${}_BF$, from which we can derive the following conclusions:

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*It will be remembered that in §16.2 we found that the von Bertalanffy growth equation fitted to adult plaice gave a fair representation of the growth of pre-recruits from one year onwards, but we have no information about the natural mortality of this phase.

(i) Because of the very short fishable phase before migration to the older phase of the population occurs, ${}_AY_W/R$ increases for all values of ${}_AF$ within the 'working range', and of course is independent of ${}_BF$.

(ii) However, any increase in ${}_AF$, whatever the value of ${}_BF$, causes ${}_BY_W/R$ to decrease through reduction in numbers of recruit migrants to the older phase of the population.

(iii) $({}_BF)_{\max}$ is independent of ${}_AF$, because variations in the number of recruits do not affect the value of $(F)_{\max}$ in a curve of Y_W/R. Consequently, the competitive influence of fleet A does not alter the conditions governing the possible value of regulation on the part of fleet B, except when economic factors are considered. From this latter point of view, the greater the value of ${}_AF$ the lower would be the fishing intensity required by fleet B to enable it to operate at the maximum profit level, owing to the decreased number of annual recruits to the adult phase of the population.

Because of the spatial segregation of the two exploited phases of the population, the quantitative aspect of these conclusions may require revision after complications such as the density dependence of parameters have been taken into account*. Qualitatively, these conclusions are likely to be sound and we must regard any exploitation of the younger phase of the population as detrimental to the yield obtained from the main exploited phase and also to the total yield, except when the fishing intensity on the older phase is very low. In general, therefore, adequate protection of clearly-defined nursery areas must be treated as an important aspect of fishery regulation, as was mentioned in §19.2.1.

19.3.2 *Equivalent regulation*

We have previously mentioned that conditions exist in an unregulated fishery, even though only one fleet may be operating, that tend to result in exploitation becoming too ntense. The above analysis shows that when there is competition between two or more fleets that are fishing the same population the tendency towards over-fishing and unprofitable exploitation is likely to be further hastened, and circumstances are less conducive to attempts at regulation on the part of any one of the competing fleets. The only satisfactory solution to the problem of regulating an international fishery therefore lies in each nation contributing to the regulation of the fishery as a whole.

The question of deciding the particular regulative procedures to be adopted by each participating nation is essentially a matter to be settled by agreement, but it may be that some objective criterion would be sought on which to assess the equivalence of the various methods proposed, in terms of their contribution to the general programme of regulation. There seem to be two main possibilities here. One is that since the immediate effect of any kind of regulation is to cause some loss of yield, the regulations adopted should result in the yield to the various nations during the transitional period, and especially in the first transitional year, being the same fraction of the yields that would have been obtained in the absence of regulation; this is equivalence based on equality of initial sacrifice. The other criterion is that the eventual benefits of the general regulation should be shared equitably among the participating nations. This equivalence of final benefit might, for example, be satisfied by each nation regulating so as ultimately to increase its yield, or perhaps the value of its yield, in the same proportion; or, since regulation may not necessarily involve an increase in yield (i.e. if the desired change is from one point on a eumetric curve to a lower one), the increase in catch per unit effort to each fleet could be taken as the basis of equivalence of final benefit, or a combination of both characteristics. The practical problem here is to establish the kinds of regulation that satisfy one of these or any other similar criterion of equivalence; as might be expected from the analysis of heterogeneous fishing in §19.3.1, the answers depend on whether the proposed regulative measures refer to changes in fishing intensity or gear selectivity or both, and on whether the gears in use before regulation are of the same or different selectivities.

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*One possibility is that the enhanced growth that might follow from the 'thinning' of the younger phase would actually increase the yield from the older phase. We have made some appreciation of this problem by finding the change of growth rate with density in the younger phase that would be necessary at least to maintain the yield from the older phase at its previous level. This turned out to be far greater than that observed in adult plaice (see §16.4.1.1) and is not supported by evidence from studies on young plaice (e.g. Thursby-Pelham, 1932). We are therefore in agreement with Russell (1932) who by different methods concluded that 'thinning' of a pre-recruit stock was unlikely to have any beneficial effects.

19.3.2.1 *Equivalent changes in fishing intensity*

The simplest case is when all fleets are using gear of the same selectivity and each proposes to regulate only its fishing intensity. From the analysis in §19.2.1.1 of the transitional phases following a decrease in fishing intensity, it can be concluded that if the fishing mortality coefficients generated by every fleet are decreased in the same proportion, all will suffer the same relative loss of yield in the first transitional year and will therefore be making equivalent regulation on the basis of initial sacrifice. This is true for any fleet whether large or small, and for fisheries based on one species or several caught together; it is also broadly applicable to an international fishery where each fleet tends to fish a different species. Moreover, provided that the initial loss is interpreted with reference to the yield that would have been obtained in the year in question had no regulation been made (see §19.2.1.1), this form of equivalence is independent of fluctuations in stock abundance.

Equivalence of final benefit when all fleets are using gear of the same selectivity and all propose to regulate fishing intensity is also satisfied to a large extent by each fleet making the same proportional reduction in the fishing mortality coefficient it generates. In this case the yields of any one species obtained by the various fleets that are fishing it will remain in the same ratios before and after regulation. However, owing to the fact that some species are bound to respond more to a given reduction of fishing intensity than are others, the *total* yields obtained by the fleets after regulation will not remain in exactly the same ratios; for example, the total yield to the fleet that happens to concentrate most on the species giving the greatest response will increase relatively more than those of the remaining fleets. These differences are unlikely to be very large, however, and if equivalence is based on catch per unit effort instead of yield the differences will be relatively even smaller, since increases in catch per unit effort will be due mainly to the decrease in effort (which is by definition of the same relative magnitude in each fleet) rather than to an increase in yield.

Although it is theoretically possible to calculate the necessary small adjustments in each nation's reduction of intensity to preserve exact equality of final benefit in terms of total yield, it is doubtful whether this would be worthwhile because there is certain to be some redistribution of effort after regulation to take advantage of the species that have responded most. The only technical problem with this kind of regulation is to relate various proposed methods of reducing fishing effort to their effect on the fishing mortality coefficient. It is here that the direct methods of reducing fishing effort discussed in §19.2.1.1 are particularly advantageous, since it would be virtually impossible to predict the exact equivalence of the indirect methods (i.e. catch limits or closure).

19.3.2.2 *Equivalent changes in gear selectivity*

We now consider the problem of assessing equivalence when all fleets are initially using gear with the same selectivity and all propose to regulate by increasing this selectivity. This is simple as far as the yields of any one species obtained by the various fleets are concerned; provided the size of mesh used by each fleet is increased by the same amount the transitional losses and final gains will be in the same proportion to each fleet, irrespective of the fishing intensity exerted by it. If, however, each fleet derives the main part of its yield from a different species there is no such simple standard of equivalence, since the effect of a given increase in size of mesh, unlike that of a reduction in fishing intensity, may differ greatly from one species to another. The effect of an increase in mesh size of say 10 mm. is, for example, much more pronounced for whiting or sole than for cod or plaice. In such cases it would therefore be necessary to assess equivalence by computing the increases in mesh size that produce the same effect on the yield of the various species concerned, although those that give equivalence of initial sacrifice will not, in general, produce equivalence of final benefit also.

19.3.2.3 *Equivalence between changes in fishing intensity and gear selectivity*

The most complex case arises either when the fleets are not initially using gear of the same selectivity, or, if they are, when some propose to regulate by reduction of fishing intensity and others by increase of gear selectivity. If the criterion of initial sacrifice is taken as the basis of equivalence it is possible to use the transition equations developed in §8.2 for assessing roughly equivalent regulative measures in these cases. This is because the changes in size and structure of the stock are not great in the first transitional year following a change either in fishing intensity or gear selectivity, as can be seen from the catch per unit effort histograms of Figs. 19.10 to 19.17. For example, if two fleets are exploiting the same population and one proposes to regulate by reduction of fishing intensity and the other by increase of gear selectivity, the initial loss of yield to each is largely independent of the change made by the other. There is, of course, no absolute standard of equivalence between decreases in fishing intensity and increases in mesh size even for one particular species, and still less so for different species; it would, for example, be necessary to know the total fishing mortality coefficient before regulation in order to use transitional yield equations in this way.

When the steady state is reached after regulation, the reciprocal effects of the different regulative methods by the various fleets can be assessed by means of heterogeneous fishing theory. To illustrate the methods required we consider a particular species exploited by independent fleets each using gear of different selectivity. The yields obtained by each fleet before regulation are then defined by the family of equations

$$\begin{aligned} {}_1Y_{W0} &= {}_1\phi({}_1F_0, {}_2F_0, \ldots\ldots {}_rF_0\,;\, {}_1t_{\rho'0}\,, {}_2t_{\rho'0}, \ldots\ldots {}_rt_{\rho'0}) \\ {}_2Y_{W0} &= {}_2\phi({}_1F_0, {}_2F_0, \ldots\ldots {}_rF_0\,;\, {}_1t_{\rho'0}\,, {}_2t_{\rho'0}, \ldots\ldots {}_rt_{\rho'0}) \\ &\vdots \\ {}_rY_{W0} &= {}_r\phi({}_1F_0, {}_2F_0, \ldots\ldots {}_rF_0\,;\, {}_1t_{\rho'0}\,, {}_2t_{\rho'0}, \ldots\ldots {}_rt_{\rho'0}) \end{aligned} \qquad \ldots\ldots (19.7)$$

the suffix $_0$ designating pre-regulation parameters and each individual equation being expressed in full by (8.13) and (8.14). Let us now suppose it is agreed that equivalence of final benefit is to be based on the criterion that each fleet shall increase its yield in the same proportion. The fractions that the yield obtained by each fleet are of the total yield, Y_{W0}, of that species before regulation can be written as

$$\begin{aligned} {}_1y &= \frac{{}_1Y_{W0}}{\sum_{i=1}^{r} {}_iY_{W0}} = \frac{{}_1Y_{W0}}{Y_{W0}} \\ {}_2y &= \frac{{}_2Y_{W0}}{Y_{W0}} \\ &\vdots \\ {}_ry &= \frac{{}_rY_{W0}}{Y_{W0}} \end{aligned} \qquad \ldots\ldots\ldots\ldots\ldots (19.8)$$

In order that the various regulations adopted by the fleets may be equivalent they must cause the yields to remain in the same ratios, i.e. they must satisfy the equations

$$
\begin{aligned}
{}_1y &= \frac{{}_1Y_{W1}}{Y_{W1}} \\
{}_2y &= \frac{{}_2Y_{W1}}{Y_{W1}} \\
&\vdots \\
{}_ry &= \frac{{}_rY_{W1}}{Y_{W1}} \qquad \ldots\ldots\ldots\ldots \qquad (19.9)
\end{aligned}
$$

the suffix $_1$ defining the post-regulation yields obtained by each fleet. Now each equation of (19.9) contains the same $2r$ parameters, namely the fishing mortality coefficient generated by each fleet and the value of $t_{\rho'}$ corresponding to each size of mesh it uses. There are therefore $r - 1$ independent equations containing $2r$ parameters, but provided each fleet wishes to change either its fishing intensity or its mesh size but not both together, then r of these will be constants. If the value of any one of the remaining r parameters is specified there will be left $r - 1$ unknown parameters for which solutions can be obtained from the $r - 1$ equations. Thus for any proposed regulation by one fleet it is possible to determine the changes in either fishing intensity or gear selectivity that must be made by the remaining fleets to satisfy equivalence of final yield. Changes that are equivalent in terms of catch per unit effort can be computed in the same way, using the quantity Y_W/F in place of Y_W in the above equations.

We have made some trial assessments of equivalence using these methods, taking the simple case of a species exploited by two fleets that are initially using the same size of mesh but one of which wishes to regulate by reduction of fishing intensity and the other by increase of mesh. This has given one result that appears to have some general significance, namely that the increase in mesh size by one fleet that is equivalent in terms of yield to a given reduction in intensity by the other is only slightly affected by the relative sizes of the two fleets. Since the same is broadly true for equivalence based on initial sacrifice of yield, it follows that either criterion of equivalence will lead to roughly similar requirements over a wide range of relative fleet size. Equivalent fishing intensity and mesh regulations based on yield are, however, likely to differ considerably from those based on catch per unit effort, especially if equivalence is defined in terms of initial sacrifice.

In summary, it can be concluded that the principle of equivalent regulation of an international fishery, as we have outlined it, can be satisfied in terms of regulation of fishing intensity, gear selectivity and, within limits, of combinations of both methods. It should not be overlooked, however, that equivalence between reductions in fishing intensity and increases in gear selectivity will probably lead to more than one size of mesh being used for a species, and this can never produce as great a yield as using the eumetric mesh size. Again, as mentioned in §19.1.5.3, the best results from an area containing a number of species whose distributions do not overlap too much can only be obtained by composite regulation, with fishing intensities and gear selectivities suited to the particular requirements of each major species or groups of species that constitute a reasonably well defined fishery. Such an objective could not be attained if it were insisted that the benefits of regulation must be shared equally among all the participating nations. Nevertheless, the concept of equivalent regulation may be of value in an international fishery when the interests of the participating countries are to some extent conflicting, and substantial progress in regulation could not otherwise be achieved.

SECTION 20: REQUIREMENTS FOR THE REGULATION OF THE NORTH SEA DEMERSAL FISHERIES

As is stated in the Introduction to this paper (§1), our main aim has been to set up and examine the properties of theoretical models of exploited fish populations as a means of gaining a further understanding of the dynamics of commercial fisheries, with special reference to the principles and methods of fishery regulation.

Pursuing this objective has led us to cover a number of different aspects of fishery research, and in some cases the problems and data involved have been sufficiently complex to require considerable digression from the main theme. For the most part these digressions form the subject of individual sections or sub-sections, and they can be located by reference to the contents list given at the beginning of the paper, while the bearing of conclusions drawn from them on the dynamics of the North Sea plaice and haddock fisheries has been summarised in §18.8. We have still to complete, however, the task allotted to us, namely to establish as far as possible the requirements for regulation of the North Sea demersal fisheries as a whole.

It will be appreciated that a detailed statement of regulative requirements to provide the basis for administrative action must refer to conditions at the time when regulation is about to be undertaken. The procedure we adopted is therefore to assess the requirements with reference primarily to the pre-war steady state from which the greater part of the data in this paper is drawn. The indications from recent years are that the post-war steady state does not seem likely to differ greatly from the pre-war one, but certain relevant changes are noted in §20.3.

There are, of course, matters of policy and administration to be considered in formulating a detailed plan of regulation, especially for an international fishery such as that of the North Sea. Many of these are outside our scope and are more appropriately discussed at a conference table than in a scientific paper, but we believe that our investigations have succeeded in their aim of defining the possibilities and limits within which the practical details of useful regulation can be constructed. To present these it will be necessary to refer to many of the conclusions that have been reached earlier, so that this last section, provides in some measure a summary of the whole paper from the practical aspect.

20.1 CHOICE OF REGULATIVE PROCEDURE FOR THE NORTH SEA— COMPOSITE OR UNIFORM REGULATION

In §19.1 we put forward the concepts of eumetric and optimum fishing as the ultimate objectives that regulation should be designed to achieve, the former being applicable to any fishery in which the selective properties of the gear can be varied so as to change, in a reasonably definite and predictable way, the age at which fish enter the exploited phase. Hence the concept of eumetric fishing is applicable in principle to regulation of the North Sea demersal fisheries, where trawl and seine are the main types of gear used, and it is clear that practical regulation should concern alteration of the fishing intensity and the selective properties of the gear so as to result in the desired adjustment of the fishing mortality coefficient F and the age of fish, $t_{\rho'}$, at which this mortality first operates. The properties of theoretical models applied to plaice and haddock, the results of which are summarised in §18.8, show clearly that the reason for the unfavourable exploitation of these fisheries during the inter-war period was partly that fishing was not eumetric—specifically, the mesh size was too small for the fishing intensity exerted—and partly that the latter was in any case too high to enable anything approaching the maximum profit to be obtained. There is every reason to believe that the same is true for at least the majority of the other North Sea demersal species of commercial importance.

Before attempting to discuss in more detail the regulative measures required in the North Sea, there are two features peculiar to the area which must be considered. The first is that there are a number of commercially valuable species of fish in the North Sea, which are caught by the same type of demersal gear and whose distributions overlap to some extent. Three major species can be distinguished, namely plaice, haddock and cod, with some four of intermediate importance, i.e. sole (*Solea vulgaris* (Quensel)), whiting (*Gadus merlangus* L.), saithe (*Gadus virens* (L.)), and dab (*Pleuronectes limanda* (L.)). In addition, there are nearly twenty minor species. Generally, the distribution of the gadoid species is more northerly than that of the pleuronectids, there being, for example, relatively little overlap between the plaice and haddock populations. Within each of these major groups, the degree of overlap is greater. The second feature is that the North Sea is fished by many fleets, the majority of which are of different nationalities and hence are associated with independent industries, each with its own social and economic background. Most fleets have their characteristic area of operation, which results in their tending to concentrate their activity on certain species of fish, though again the overlap is considerable in some cases. The two main types of demersal gear also tend to be used in somewhat different areas, according to type of ground and distribution of fish.

These two elements of heterogeneity, the one concerning the fish stocks and the other the fishing activity, are fundamental in viewing the question of how the North Sea could best be treated for purposes of regulation. Two main types of procedure can be distinguished. One, which in §19.1.5.3 we termed *composite regulation*, is to apply several different regulative measures on an area basis, in relation primarily to the distribution of fish, so that each major species or group of species is exploited by the particular eumetric combination of fishing intensity and gear selectivity most suited to its biological characteristics. With this type of regulation, the criteria for optimum fishing could also vary according to the special needs of the fleets concerned and their associated industries. The other procedure, which we have called *uniform regulation*, is to accept the contemporary distribution of fishing effort and to stabilise the relative fishing intensities generated by the fleets of each nation on some generally agreed basis, for example, by reference to the relative intensities during a certain period before regulation is introduced. Further regulation would then take the form of making the same proportional changes in the fishing intensity generated by each fleet, and adjusting the mesh used by each to the same size, the requirements for optimum fishing being decided in terms of the total fishing intensity and single mesh size that would give the best average result for all species and all fleets.

There is no doubt that composite regulation of the North Sea, if it could be applied, would produce better results than uniform regulation, both in terms of total yield and the conditions under which the fishing industries of each nation operate. This is so even making allowance for the fact that there is considerable overlap in the distribution of many species, and that the selectivity of existing types of fishing gear cannot be adjusted differentially according to the requirements for the various species. The main difficulty with composite regulation, and it would seem an insuperable one at the present time, is that there seems to be no way of enforcing a regulative measure, whether it involves control either of fishing intensity or of mesh size, which applies to some areas and species but not to others. Certainly, to obtain the full benefit from composite regulation would demand a degree of voluntary conformity with regulative measures on the part of fishermen and fishing industries of all nations which cannot be relied upon at present. There are, of course, all intermediates between these two main types of regulation. For example, the natural tendency for the fleets of some nations to concentrate on certain species may make it possible to have more than one size of mesh in use without raising the difficulty of enforcement, and thus to have a limited number of combinations of fishing intensity and mesh size which,though perhaps not truly eumetric, nevertheless produce better results than strictly uniform regulation. The concept of equivalence between regulation of fishing intensity and gear selectivity outlined in §19.3.2.3 may also enable some progress towards composite regulation to be achieved.

The question of which type of regulation would be most suitable as a long-term policy is not, however, a matter which need necessarily be decided upon before any action can be taken. The need in the first instance is to introduce regulation of any kind that produces changes in fishing intensity or in mesh size that are at least in the right direction. The details are clearly a matter for agreement between the nations concerned, but if the effects of regulation are to be predictable and if the full benefit is to be obtained from it, it must involve specifying and enforcing a definite fishing intensity and a definite mesh size for at least the major species, even though its purpose may be to bring about a *change* in only one of these two factors. Uniform regulation therefore suggests itself as being the simplest and most immediately practicable objective for the North Sea, and it is with this that we shall be concerned in the remainder of this section. It should leave open the possibility, at any later time, of introducing more than one size of mesh, or of adjusting the fishing intensity on a regional basis, so that the major species can be fished more nearly eumetrically. The next stage is, therefore, to predict the requirements for optimum fishing of the North Sea on the basis of uniform regulation, and for this we shall suppose that it is agreed to stabilise the relative magnitudes of the fishing mortality coefficients generated in plaice, haddock and cod during the pre-war period from 1930 to 1938. Our problem is therefore to find the proportional change in the fishing intensities of all fleets from their pre-war levels, and the single size of mesh, that would give the best results from the North Sea as a whole.

20.2 Assessments Relevant to Determining the Requirements for Optimum Fishing on the Basis of Uniform Regulation

The methods by which the requirements for eumetric and optimum fishing may be assessed when a number of different species are exploited simultaneously have been discussed in §19.1.5. Assessment is based primarily on combined eumetric value and fishing curves, in which the yields of all species are weighted according to their relative prices. In the case of the North Sea there are other relevant criteria, the most important being that the balance of species in the total yield should not be altered by regulation more than can be helped, and that there should be no drastic reduction in the yields of even minor species, since these may be relatively important to a fleet that shows decided preference for them. It will be appreciated that because relatively little is known about a large number of minor species in the North Sea, it is not possible to proceed directly to total combined value or fishing curves for all demersal species. Therefore we consider first the plaice and haddock and show that by using certain generalisations from them, together with rough assessments for cod and sole, the general picture can be established with sufficient confidence to provide the basis for at least the first stages of regulation.

20.2.1 *Combined eumetric curves for plaice and haddock*

It may be helpful first briefly to recapitulate the main features of the eumetric yield and fishing curves for plaice and for haddock, which were presented in §19.1.1. In Figs. 19.2.1 and 19.2.2 we have shown eumetric yield curves for these two species, all of which ascend to an asymptote without passing through a maximum, and in each case 90% or more of the asymptotic yield is reached at a value of F of about 0·5. These features remain even when more complex relationships such as density dependence of growth and recruitment are introduced; indeed, these have relatively little effect on the characteristics of the curves that determine the fishing intensity necessary to give maximum profit. Particularly relevant here is the fact that when growth and recruitment are made to vary together with density the resultant eumetric yield curves can be very similar to those calculated from simple models with constant parameters. On the other hand, the combinations of fishing intensity and mesh size that are eumetric, defined by the eumetric fishing curves (Figs. 19.4.1 and 19.4.2), differ appreciably in the two species and, moreover, are altered by the density dependence of parameters. This latter relation works always in the same direction, whether the density dependence is of growth, recruitment, natural mortality or combinations of these factors, and its effect is to lower the size of mesh that is eumetric with any given fishing intensity. These findings suggest that the simple model with constant parameters can give a fairly reliable indication of the shape of eumetric yield curves and hence of the fishing intensity required for optimum fishing, but that the corresponding eumetric mesh sizes are always overestimated by using constant parameters.*

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*This is because the parameter values we have used in the simple model happen to have been estimated from a steady state in which the density was considerably lower (and hence the growth correspondingly higher) than at any point on the eumetric yield curve. If the parameters had been estimated during an early phase of exploitation when the density was higher than with eumetric fishing, the converse would have been found.

Bearing these points in mind we now proceed to the combined eumetric value curve for plaice and haddock. Since individual eumetric yield curves are not additive, this is derived from the original yield-isopleth diagrams for each species (Figs. 17.14 and 17.26) in the usual way, but with the yield of each weighted according to its relative price. For the price of North Sea plaice and haddock we have used data for the years 1930-1938 given in the I.C.E.S. Bulletin Statistique; these give mean price indices of 0·685 and 0·374 shillings per kilo respectively. Because we have no information on the density dependence of parameters in species other than plaice and haddock, the procedure we adopt from now on is to construct combined eumetric curves using constant parameters. The findings of §18 and the generalisations deduced above for plaice and haddock separately will be used in §20.2.3 to make some allowance for the probable effects of density dependence.

The combined eumetric value curve for plaice and haddock is shown in Fig. 20.1 (curve P + H). In this and subsequent eumetric value diagrams the ordinates are expressed for convenience in shillings × 10^{-7}, and it is important to note that this is not equivalent to the proper transformation of yield into value taking into account the change in price with the various characteristics of yield, as discussed in §19.1.3.2; it implies merely that the *relative* price of the species concerned remains constant (see also §20.2.3). The abscissae show the proportional changes in the fishing mortality coefficients of both species from their mean pre-war values, which were estimated in §§13.2 and 14.3.2 as 0·73 in plaice and 1·0 in haddock. For brevity, we denote the abscissae by the symbol I; thus a value of I of 0·5, for example, implies a reduction in total fishing intensity to about a half of the pre-war level, and corresponds to a value of F of 0·365 in plaice and 0·5 in haddock.

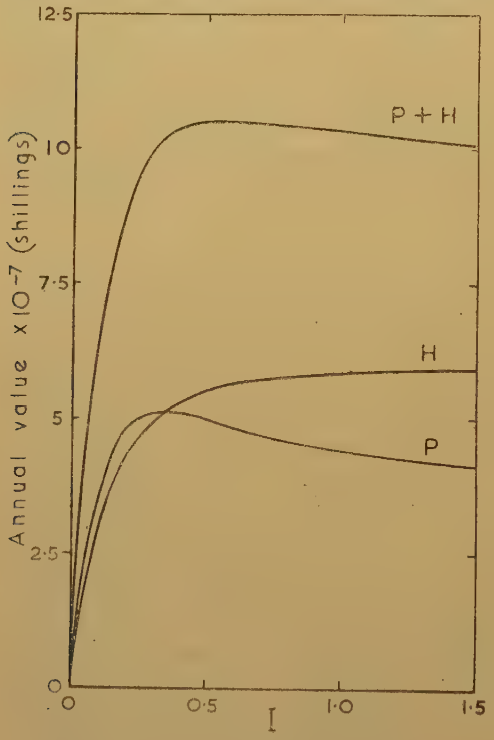

FIG. 20.1 PLAICE AND HADDOCK: COMBINED EUMETRIC VALUE CURVE

[Combined eumetric value P + H as a function of fishing intensity relative to the mean pre-war level in each species (I). This and subsequent combined value curves of §20 are derived by summing the yield of each species weighted by its mean pre-war price, as explained in the text. The contribution of each species to the combined curve P + H is shown by curves P and H for plaice and haddock respectively.]

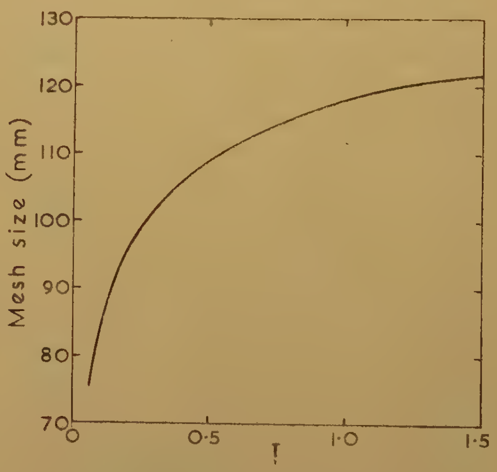

FIG. 20.2 PLAICE AND HADDOCK: COMBINED EUMETRIC FISHING CURVE

[This defines the relation between fishing intensity (as a ratio of the mean pre-war level, I) and mesh size used to construct the combined eumetric value curve P + H of Fig. 20.1.]

It will be seen that plotting curves against I is fundamentally the same as plotting against F, and is merely a convenient way of expressing stabilisation of the ratios of the fishing mortality coefficients for the species concerned, which is the basis of uniform regulation.

The curve of Fig. 20.1 differs from any eumetric curve for either species alone in that it reaches a maximum, at a value of I of about 0·5; furthermore, the curvature is largely restricted to a range of I between about 0·3 and 0·5, so that about 90% of the maximum is reached at about one-quarter of the pre-war fishing intensity. The existence of a maximum in this combined curve is the result of it being a compromise between the differing requirements for the two species; in order to avoid a serious drop in the yield of haddock the range of mesh size is limited, and in these circumstances the contribution of plaice is greatest at low values of F (and hence of I), and is in fact sufficiently marked to generate a maximum in the combined yield curve. The contribution of each species to the combined curve is shown by the curves P and H of the same figure; it will be noted that at low values of I the proportion of each species is about the same, but at high values the contribution of haddock exceeds that of plaice.

The eumetric fishing curve corresponding to the combined eumetric value curve P + H of Fig. 20.1 is shown in Fig. 20.2. This is similar in shape to those for each species separately (curves P_1 and H_1 of Figs. 19.4.1 and 19.4.2) and over the critical range of I between 0.25 and 0·5 the eumetric mesh range is seen to be between about 95 and 110 mm.

It is of interest to note, in passing, the extent to which the combined eumetric curve for plaice and haddock of Fig. 20.1, which is the best that can be obtained with uniform regulation, falls short of the curve that could be reached if it were possible to fish each species according to its particular eumetric requirements. This can be constructed by adding the independent eumetric yield curves P_1 and H_1 of Figs. 19.2.1 and 19.2.2, weighted by the same relative price indices as used above, and is shown as curve (a) of Fig. 20.3 with combined eumetric value curve P + H of Fig. 20.1 shown as curve (b) for comparison. It is seen that while at values of I less than 0·2 the two curves are almost identical, curve (a) is about 20% higher at half the pre-war fishing intensity and the difference gradually increases at higher values of I.

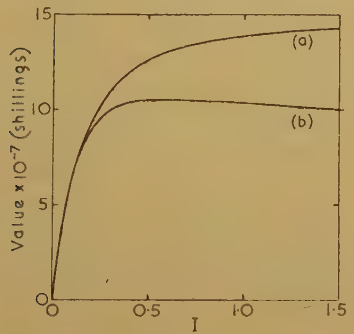

FIG. 20.3 PLAICE AND HADDOCK: COMBINED AND SUMMED EUMETRIC VALUE CURVES

[The combined curve (P + H) of Fig. 20.1 is shown here as (b); in curve (a) the separate eumetric yields of each species from Figs. 19.2 are summed (after weighting by price), implying the use of a different eumetric mesh size in each fishery (i.e. composite regulation).]

20.2.2 *Modifications required by inclusion of cod and sole*

The other major species in the North Sea is cod; including this with plaice and haddock accounts for some 60% of the total demersal catch. No other single species compares in importance with these three, but it is not possible to deduce the requirements for uniform regulation of the North Sea without reference to the minor species.

It so happens that the latter fall into two main groups on the basis of size. Thus some, such as saithe (*Gadus virens* (L)), turbot (*Rhombus maximus* (L)), brill (*Rhombus laevis* (Rondelet)) and skate (*Raia* spp.), probably require eumetric mesh sizes similar to those for cod, while the eumetric mesh sizes for others such as whiting and sole are rather smaller, at any given fishing intensity, than that for haddock. The yield of the larger species of the minor group is therefore adequately safeguarded by inclusion of cod which, because of its relative importance, has an appreciable influence on the total eumetric curves. The second group, however, need special consideration, because a combined eumetric curve that gives the greatest total value of all species together may well involve mesh sizes that greatly reduce the yield of small species that are of only minor importance. If the latter were caught only incidentally this would probably be unimportant, but sole and whiting are deliberately sought by fleets of some nations, and any regulation that caused a serious reduction in their yield may be unacceptable. Since rough assessments can be made for sole we therefore include this as representative, provisionally, of the smaller species of the minor group.

Graham (1938b) gives age-composition data for the cod during the years 1931 to 1936 from which a mean estimate of the total mortality coefficient ($F + M$) is 0·76. In the absence of any known predator on adult cod, and in view of the fact that the cessation of fishing during the two world-wars caused changes of the same order of magnitude in cod as in plaice, we have taken a value of M of 0·1. Thus our best estimate of the mean pre-war fishing mortality coefficient in cod is $F = 0.66$. Owing to the close similarity in shape of cod and haddock we have used the same factor relating cod-end mesh size and mean selection length in both species, i.e. $b = 3{\cdot}33$. The parameters of the von Bertalanffy growth equation fitted to growth data for cod have been determined in §16.2.3, and are $W_\infty = 20000$ gm., $K = 0{\cdot}2$ and $t_0 = 0{\cdot}28$ years. Graham (1934) has shown that although cod fry are pelagic for only 2 or 3 months they are difficult to catch even with covered trawls until about the end of their first year of life, and he suggested that this was due to their liking for stony and weedy ground unfit for trawling. In the following calculations we have accordingly taken t_ρ to be 1 year; this value may be a little too low, but this has little effect when examining the effects of changes in fishing intensity or large changes in gear selectivity, as we shall be doing in this section. It is, however, a question that needs further mention in §20.3 where the effects of a change in mesh from 70 to 80 mm. are examined, since this involves a change in mean selection length that lies within the critical range where codling may not be fully exposed to fishing. Finally, we use a value of $t_\lambda = 15$ years, as in plaice, and a pre-war price index, obtained in the same way as those for plaice and haddock above, of 0·402 shillings per kilogram.

The von Bertalanffy equation has been fitted to growth data for sole in §16.2.3, giving the parameter values $W_\infty = 482$ gm., $K = 0{\cdot}42$, $t_0 = 0{\cdot}3$ years. From a summary of the published selection data for sole, Jensen (1949) deduced a value of b of 3·65, which is in harmony with experimental results obtained recently by the Lowestoft Laboratory.* A difficulty is that no adequate age-composition data for sole appear to have been published. Baerends (1947) has expressed the opinion, however, that the natural mortality of sole is low; certainly there is no evidence to suggest that there is any major predator of sole within the commercially important range of size. Hence by assuming a value for sole of $M = 0{\cdot}1$, the same as in plaice, it does not seem likely that we are underestimating the magnitude of this parameter. The fact that sole is a much sought fish and that its distribution overlaps that of plaice to a great extent suggests that the value of F is also similar to that in the latter species. On the other hand, a sole may be able to avoid capture more readily than a plaice, so that for the following assessments we assume a value for sole of $F = 0{\cdot}6$, i.e. a little smaller than in plaice.

Using the above estimates we now incorporate the requirements for cod and sole in the combined eumetric curves obtained previously for plaice and haddock, dealing first with cod. We have previously drawn attention to the fact that the mesh sizes required for eumetric fishing of plaice alone are larger than those for haddock, and this is of course due to the more rapid increase of weight with age in the former species and to its greater girth at a given weight. The growth of cod is much more rapid than that of plaice, and as a consequence the curves giving the combined value of plaice, haddock and cod as a function of mesh size at a given value of I have two maxima, examples for $I = 0{\cdot}275$ and $I = 0{\cdot}685$ being shown in Fig. 20.4. In the first of these maxima the three species are present in roughly equal quantities; at larger mesh sizes the haddock begins to disappear from the catch—causing the minima in the curves—while the second maxima are caused almost entirely by plaice and cod. Now, if the simple criterion of maximum total value is taken to

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*See Margetts (1955) who obtained a value of $b = 3{\cdot}5$ for cod-end meshes in the region of 85 mm.

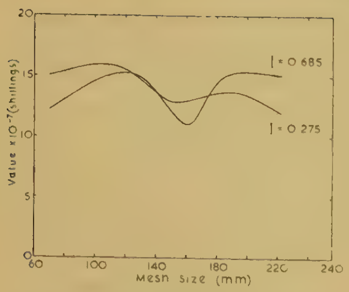

FIG. 20.4 PLAICE, HADDOCK AND COD: COMBINED VALUE AGAINST MESH

[Combined value as a function of mesh size for two different values of I, showing the two maxima. The first of these is used to construct the restricted eumetric value curve $(P + H + C)_e$ of Fig. 20.5 since all three species contribute to it in roughly equal amounts; the right-hand peaks are caused almost entirely by plaice and cod.]

define the eumetric mesh sizes, it is seen that while at low values of *I* (e.g. $I = 0{\cdot}275$) mesh sizes corresponding to the first set of maxima would be chosen (115-120 mm.), at higher values of *I* (e.g. $I = 0{\cdot}5$ and above) it would be necessary to take mesh sizes corresponding to the second set of maxima (180-200 mm.). However, because of the need to maintain variety in the total catch, especially of major species, it is unlikely that the very large meshes associated with the second maxima would be acceptable; not only would there be very little haddock in the catch but smaller fish such as whiting and sole would be completely lost. Hence to arrive at eumetric combinations of fishing intensity and mesh size that produce the best compromise for the three species together, it is necessary to impose some form of 'external' restriction on the size of mesh which may be considered, that is, to derive restricted eumetric curves in the sense defined in §19.1.5.3.

The most obvious procedure as far as the three major species are concerned is to exclude the second set of maxima entirely and to define restricted eumetric curves in terms of the values and mesh sizes associated with the first set of maxima; this limits the mesh

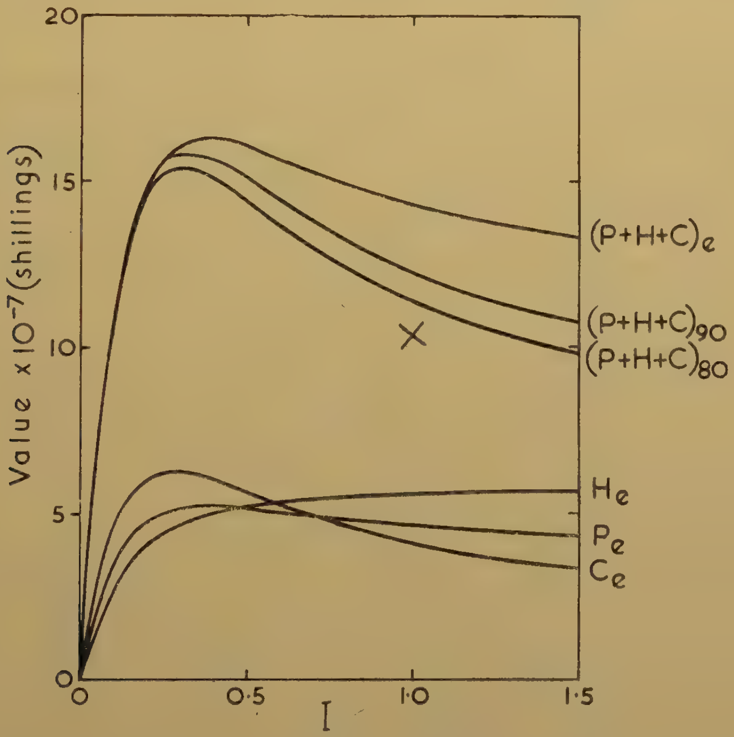

FIG. 20.5 PLAICE, HADDOCK AND COD: COMBINED EUMETRIC VALUE CURVES

[Combined eumetric value as a function of fishing intensity (ratio of mean pre-war level, I) with three kinds of restriction on the range of mesh. Curve $(P + H + C)_e$ is based on the first maxima of curves such as those of Fig. 20.4; in curve $(P + H + C)_{90}$ the mesh is restricted to an upper limit of 90 mm.; in curve $(P + H + C)_{80}$ the upper limit of mesh is 80 mm. The components of $(P + H + C)_e$ are shown by curves P_e, H_e and C_e, respectively. The total value of the mean pre-war yield of plaice, haddock and cod is shown by the cross.]

size to below 130 mm. over the whole range and avoids any drastic changes in the balance of the three species in the yield. The resulting combined eumetric value curve is shown in Fig. 20.5 curve $(P + H + C)_e$, in which the fishing intensities on plaice, haddock and cod are in the proportions 0·73 : 1·0 : 0·66 respectively. It is seen that the features in which the combined curve for the plaice and haddock (Fig. 20.1) differs from those for either of these species alone become even more pronounced when cod is included. Thus the combined curve of Fig. 20.5 has a well-defined maximum, and this occurs at a lower value of I than that of Fig. 20.1, i.e. at about 0·4 or some two-fifths of the pre-war intensity. As before, this is the result of including a fish—cod in this case—the yield from which increases sharply at low values of I with the relatively small mesh sizes needed to maintain the yield of haddock. This is seen most clearly by the individual yield of the three species corresponding to the combined curve $(P + H + C)_e$ which are shown by the curves P_e, H_e and C_e of Fig. 20.5. The eumetric fishing curve corresponding to the combined eumetric value curve $(P + H + C)_e$ of Fig. 20.5 is shown by curve (e) of Fig. 20.6. From this it is seen that at a value of I of 0·4, corresponding to the maximum of the value curve, the eumetric mesh size is about 114 mm.

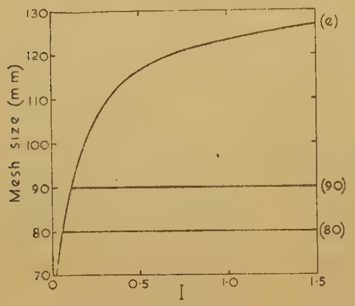

FIG. 20.6 PLAICE, HADDOCK AND COD: COMBINED RESTRICTED EUMETRIC FISHING CURVES

[These define the relations between fishing intensity (as a ratio of the mean pre-war level, I) and mesh used in constructing the combined eumetric value curves of Fig. 20.5, and are labelled (e), (90) and (80) to correspond.]

The total value of North Sea sole is only in the order of 5%-10% of the total demersal catch, so that including this species in the combined eumetric value curve of Fig. 20.5 would have no appreciable effect. Therefore it is necessary to deal with the requirements for sole on the basis of uniform regulation in a different way, the first question being to find what effect on the yield of sole would be caused by operating at various points on the eumetric fishing curve (e) of Fig. 20.6. This is shown in Fig. 20.7, where the yield per recruit of sole is plotted against I, assuming the pre-war mean value of F to be 0·6 and using mesh sizes varying with I according to curve (e) of Fig. 20.6. The value of Y_W/R corresponding to the estimated pre-war conditions ($F = 0{\cdot}6$, mesh size = 70 mm.) is shown by the horizontal broken line at the top of the diagram, and it is at once clear that at no point on the eumetric fishing curve for the three major species is the yield of sole as high as the pre-war level. The highest point is about 55% of the pre-war figure, and this occurs at a value of I about 0·15; however, at this low I the yield from the three major species would be well below its maximum, and such a drastic reduction in fishing intensity would probably be unacceptable for other reasons (see §19.1.4).

Now the reason why the sole yield curve of Fig. 20.7 never reaches the pre-war level is that before the fishing mortality becomes at all high, the mesh sizes specified by the requirements for the three major species have become too large to enable even the largest sole to be retained by the gear; as a result the yield of sole falls to zero at a value of I about 0·2, corresponding to a mesh of about 102 mm. This suggests that an alternative way of reconciling the desire to obtain the best possible results from the major species whilst avoiding any serious loss of sole would be to fix an upper limit to the permissible range of mesh size; we now need to estimate this limiting mesh size and to find to what extent it would affect the yield of major species.

Fig. 20.8 shows curves of Y_W/R for sole plotted against mesh size for various values of I, with the estimated pre-war value indicated by the point S. From these curves it can be concluded that at the relatively low values of I needed to obtain the best results from the major species (i.e. 0·3 to 0·5) the size of mesh is not critical within the range 70 to 90 mm.,

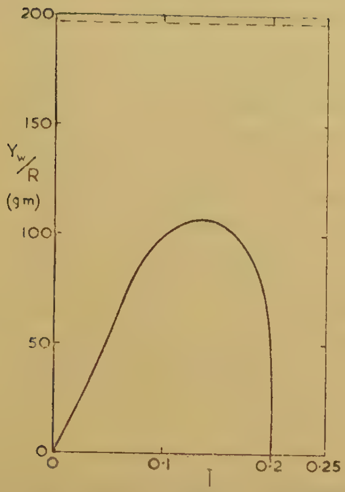

FIG. 20.7 SOLE: YIELD AGAINST FISHING INTENSITY, MESH SIZE VARYING

[Yield per recruit, Y_W/R, as a function of fishing intensity (ratio of mean pre-war value, I) with mesh size varying according to curve (e) of Fig. 20.6. The mean pre-war value of Y_W/R is shown by the horizontal broken line. The yield falls to zero at I = 0·2 corresponding to a mesh of about 102 mm.]

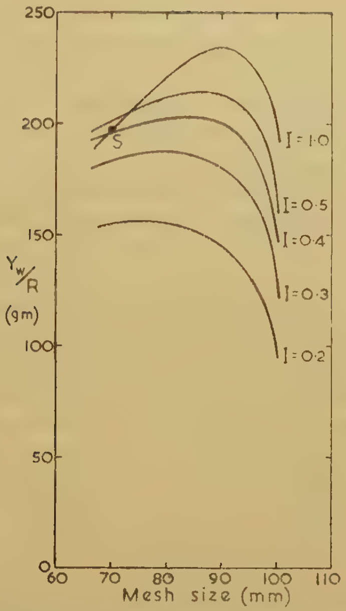

FIG. 20.8 SOLE: YIELD AGAINST MESH AT VARIOUS FISHING INTENSITIES

[Yield per recruit, Y_W/R, as a function of mesh for various values of fishing intensity (ratios of mean pre-war value, I). The mean pre-war value of Y_W/R is shown by the point S at a mesh of 70 mm. on the curve for I = 1·0.]

but the yield falls steeply thereafter. Hence the maximum mesh needed to maintain the yield of sole at about the pre-war level must certainly not be greater than 90 mm., and to find the effect of this on the major species it is necessary to redefine the restricted eumetric value curve for them with this upper limit of mesh size. Actually, this amounts to deriving a combined value curve with the mesh constant at 90 mm. for all values of *I* greater than about 0·1, since the new restricted eumetric fishing curve becomes horizontal at this value of *I*, as shown by curve (90) of Fig. 20.6. The combined value curve for plaice, haddock and cod, restricted to a 90 mm. mesh limit, is shown by curve $(P + H + C)_{90}$ of Fig. 20.5. It is considerably below the previous curve at high values of *I* but has a maximum only slightly lower, although this occurs at a slightly lower value of *I* (about 0·3). This shows that at values of *I* in the region of 0·3 the catch of the major species is not critically dependent on the size of mesh. In fact, even an 80 mm. mesh would cause an additional loss of only about 3% of their maximum value compared with a 90 mm. mesh, as can be seen from curve $(P + H + C)_{80}$ of Fig. 20.5, which is the combined value curve for plaice, haddock and cod with the upper limit of mesh size restricted to 80 mm. Hence by using a mesh of 80 to 90 mm. and a value of *I* of 0·3 to 0·4, it should be possible to maintain the yield of sole and at the same time bring the value of the major species to somewhere near its potential maximum. The exact balance would of course be a matter to be decided by the nations concerned, but relevant here is the fact that in these circumstances the catch per unit effort of sole would be in the order of twice its former value, and make fishing for this species much more profitable even for a fleet that tended to seek specially for it.

20.2.3 *Allowances for density dependence and some other factors*

The curves of Figs. 20.5 and 20.6 are derived from simple models with constant parameters, so that there is the question of whether the density dependence of parameters would appreciably alter their shape and the conclusions we have drawn from them. With a combined eumetric yield curve, and especially one in which the permissible range of mesh size is restricted, the differences in density of any one of the constituent species at various points along it are more pronounced than in a eumetric yield curve constructed for that species alone, but are less than if the mesh were held constant throughout*. The effects of density dependence of parameters on yield curves for plaice and haddock with the mesh constant, which we examined in §18, therefore give some idea of the maximum differences that might be expected between the combined value curves of Fig. 20.5 and the true curves. It will be remembered that yield-intensity curves were found on the whole to be relatively insensitive to the influence of density dependent changes, the exception being when the recruitment increases markedly with relatively small increases in density from the observed state, and there is no available evidence to suggest that this would happen, at least in plaice and cod. It therefore seems entirely probable that the true combined value curve would reach a maximum at a value of I only a little higher than that shown in Fig. 20.5 and therefore still considerably less than unity. The findings of §18 suggest, in fact, that the maximum would probably occur somewhere within the range $I = 0{\cdot}3$ to $0{\cdot}6$.

We can also be fairly sure that the mesh sizes defining the eumetric fishing curves of Fig. 20.6 are larger than those which would result if the density dependence of parameters could be taken into account. Again, however, the severe restriction of mesh range that has been necessary means that the differences will not be as large as those in the eumetric fishing curves for either plaice or haddock alone. Although we can give no precise figures, the mesh sizes of the true eumetric fishing curve for the three major species together (i.e. that taking account of density dependence) are probably some 10 to 20 mm. lower than those defined by curve (e) of Fig. 20.6 over most of its range. Similarly, the upper limit of mesh size needed to maintain the yield of sole at any desired level will also have been overestimated by assuming parameters to be constant in this species if actually they are density dependent. With a mesh restriction of this kind, however, reduction of fishing intensity will be the main cause of density increase; hence any error in estimates of mesh size for sole that might be involved through using constant parameters does not arise until fishing intensities substantially below the pre-war level are considered.

The effects of changes in density also have an important bearing on the true level of the maxima in the curves of Fig. 20.5, and hence on estimates of the potential increase in value of the three major species, compared with pre-war conditions, that these maxima imply. An indication of the increase that might be expected can be gained by reference to the point on Fig. 20.5 at $I = 1{\cdot}0$ indicated by a cross, which shows the combined average pre-war yields of plaice, haddock and cod, weighted by the same pre-war indices of value to permit comparison with the value curves of the same figure. It is seen that the use of constant parameters results in a prediction of the maximum combined value of these species some 50 to 60% higher than the pre-war level. Now the stock density at the maximum of the value curves would be several times greater than that during the pre-war period, and whether the true increase in value would be as much as 60% depends largely on the effect that this greater abundance would have on recruitment into the major species. This is a point on which we have no definite information, but a minimum estimate of the increase in value can be obtained by analogy with the results obtained in §18.5.1 from population models in which growth and natural mortality are taken as density dependent but recruitment is assumed constant. These suggest that a decidedly conservative estimate of the increase in yield would be about one-third of that predicted by using constant parameters, i.e. an increase above the pre-war level of some 15 to 20%. If it should turn out that the recruitment increased appreciably, it is of course possible that the actual increase in value could be as much as that predicted with constant parameters, or even more. As mentioned earlier, the minor species making up the remainder of the total catch differ greatly in size; hence their inclusion is not likely to alter appreciably the shape of the value curves for the major species, and the latter can reasonably be taken as representative of the behaviour of the total demersal catch until evidence to the contrary becomes available.

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*It will be remembered from §19.1.1 that the changes in fishing intensity and mesh size defined by a eumetric fishing curve for a single species are such as to maintain a nearly constant density throughout the range of fishing intensity (see Fig. 19.3).

Mention must also be made of the fact that although we have for convenience referred to the curves shown in this section as eumetric value curves, in reality they take into account only the relative values of the species concerned. Constructing a true eumetric value curve as defined in §19.1.4 is essentially an economic problem that we cannot attempt to consider in detail, but some general statements can be made. Thus there is no reason to believe that a sustained increase in yield of North Sea demersal fish in the order of 20% above the pre-war level would saturate consumer demand. Again, since this maximum yield corresponds to a reduction of the fishing mortality to about half its pre-war value the annual fluctuations in yield would be noticeably less, which might tend to counteract any fall in demand. With a yield curve in which the mesh is constant for nearly the whole of its extent, the average size of fish in the catch would increase considerably with a reduction of fishing intensity*; in the present case this is probably the factor that would have the greatest effect on the price of fish. It therefore seems reasonable to suppose that the average price of fish would tend, if anything, to increase with a reduction of fishing intensity to the order of half its pre-war level, which would to some extent counteract the effect of density dependence in tending to raise the value of I at which the maximum occurs.

The conclusion that there is a maximum in the combined value curve for the North Sea demersal species at a fishing intensity considerably below the pre-war level is of immediate relevance to the question of determining the requirements for optimum fishing. It means, firstly, that the benefits to be expected from reduction of fishing intensity, over a substantial range, are not only those of greater economic efficiency but of increased yield as well. Secondly, it follows that the maximum potential profit point is at a value of I less than that corresponding to the maximum of the value curve (see §19.1.5.2). How much below the latter the point of maximum profit lies cannot be estimated accurately without a detailed analysis of economic factors, but in curve $(P + H + C)_{90}$ of Fig. 20.5, for example, it is seen that decreasing the fishing intensity from one-third of its pre-war level to one-quarter would entail a negligible loss of value, but it might enable running costs to be cut by up to 30% if accomplished in the most economical way. It is worth noting that although we concluded above that the true combined value curve probably has a maximum at a higher value of I than those of Fig. 20.5, at the same time the indications from the yield curves of §18 are that it will also be flatter. If this is so, the effect of density dependent changes on the maximum potential profit point will probably be slight.

20.2.4 *Summary*

We have now discussed most of the factors determining the requirements for optimum fishing of the North Sea which are open to direct analysis and of which we can make some quantitative assessment. It is scarcely necessary to emphasize again that in the present state of knowledge our predictions of the results of extensive changes must be interpreted with due caution. On the other hand, the experience gained during our investigations suggests that to achieve a significant improvement in the accuracy of predictions of the requirements for optimum fishing will require research and data extending over a number of years. We have in mind not only problems such as the density dependence of parameters, which require primarily research projects, but also the estimation of natural mortalities and rates of dispersion, for which more detailed and comprehensive commercial statistics are essential. There is also the fact that although a larger mesh size than 70 mm. would certainly benefit the yield of the major species, especially plaice and cod, how far it is practicable to go in this direction depends critically on the extent to which the yield of small minor species—about which relatively little is known at the present time—must be maintained. In these circumstances it is helpful to set out as a guide to action such predictions as are possible in the present state of knowledge, and our investigations lead,

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*This property should be contrasted with that of a true eumetric yield curve, in which the average size of fish in the catch *falls* as the fishing intensity is reduced (see §19.1.3.2).

without serious qualification, to certain conclusions which we believe are sufficiently reliable to establish at least the order of magnitude of the changes that would be required. These conclusions can be summarised as follows:

(a) The fishing intensity which would give the maximum potential profit from the North Sea demersal fisheries taken as a whole is considerably lower than that of pre-war years. It is unlikely to be greater than one-half of the average intensity during the years 1930-1938, and may be nearer one-third. The extent to which a decrease of this magnitude—viewed as a long-term project—would be compatible with social and political interests remains to be seen; but any advantages that there may be in not reducing the fishing intensity as much as this must be set against not only a smaller profit margin but also, over most of the range, a smaller yield as well.

(b) The cod-end mesh size, applied to all species, that is best suited to this level of fishing intensity, is unlikely to be greater than 100 mm. and is probably between 80 and 90 mm.

(c) This combination of fishing intensity and mesh size is determined primarily by the requirements for plaice, haddock and cod, which together comprise more than half the total yield. There is no reason to believe that it would affect adversely the general balance of species in the total yield, though at a later stage some minor adjustments may be necessary on account of the smallest species such as whiting and sole, depending on the extent to which some sacrifice in yield from them would be offset by the much greater profit of fishing and the greater yield from the major species.

(d) The actual increase in total value that would result in these circumstances cannot be estimated with precision. A conservative estimate would be some 20%, but it is quite possible for the increase to be 50% or even more. The value of the catch per unit effort, however, would certainly increase very considerably; thus taking even this minimum estimate of the increase in value gives a value per unit effort some three times that obtained before the war.

(e) No definite statement can be made concerning the effect of these changes on the economic state of the fishing industries, but it is certain to be profound. Some idea of the potential increase in profit can be gained by supposing that the rate of profit (i.e. the excess of value of catch over total running costs as a percentage of the latter) was 5% during the pre-war period, so that the value of the total catch can be taken as 105 units and the total running costs as 100 units. Then at the maximum potential profit point the value would probably be at least 125 units, but if the reduction in fishing intensity to about half its pre-war level was accomplished in the most economical way, e.g. by a permanent reduction in fishing power, the running costs might fall to perhaps 60 units. This represents a potential profit of 65 units, and a rate of profit of more than 100%, i.e. a twenty-fold increase over the initial figure of 5%. Such enormous increases as this would leave an ample margin to be shared between the industry and the consumer, in the form of technological improvements, better standards of living and working conditions for fishermen and a substantial reduction in the price of fish.

The conclusion that the major adjustment that would ultimately be required is a large and of course permanent reduction in fishing intensity, rather than a substantial increase in size of mesh, has two important implications. It means, in the first place, that the benefits to be obtained with optimum fishing do not depend so much on the increase in yield that would result, as in the saving of running costs that would be possible with the fishing intensity reduced to half or perhaps even a third of its pre-war level. For example, even if the yield in these circumstances were to do no more than remain unchanged, the catch per unit effort would still rise by about 100% and the potential rate of profit by perhaps 15-fold. It does not need benefits even as great as these to make regulation well worthwhile to the industry and consumer alike.

Secondly, a permanent reduction of fishing intensity to something in the order of half its present level would involve far-reaching economic and social readjustments, so that there is no question of attaining optimum fishing in one step by means of a single regulation; rather, the approach to optimum fishing is best visualised as proceeding in a series of stages extending over a number of years. This means that our inability to predict accurately the requirements for optimum fishing is no obstacle to the first steps in regulation; the immediate requirement is to institute changes in fishing intensity and gear selectivity that are in the right direction, but which are not so great that they cause temporary distress to the fishing industries.

20.3 First Steps in Regulation of the North Sea: the Probable Effects of a 15% Reduction in Fishing Intensity and an Increase of Mesh to 80 mm.

Some of the factors relevant to the framing of measures that would constitute satisfactory first steps in the regulation of the North Sea, such as the choice of method and the changes to be expected during the transitional phase, have been discussed in §§19.2.1 and 19.2.2. As far as fishing intensity is concerned, the important point is that it can be adjusted in a variety of ways; by changing either the number of ships operating or the time spent fishing by each, the latter taking the form either of a complete restriction of fishing in a close season or a spacing-out of the fishing time of each vessel more or less regularly during the year. Agreement at the international level, however, need concern only the ratios of the fishing efforts of the countries involved. The question of how a limited effort is to be administered could be left to each country to use the method most suited to its economy and the social background of its fishing industry, remembering that control of total fishing power is essential to enable the main economic benefits of regulation to be obtained, whether the latter concerns a reduction in effort or an increase in gear selectivity. For making changes in gear selectivity there is no alternative but to increase the size of mesh. As an adjunct, minimum legal size limits for fish landed, related to the selection range of each species, are necessary as a means of enforcing a mesh regulation unless direct inspection at sea on an adequate scale is practicable.

The concept of equivalence between various regulative methods discussed in §19.3.2 is clearly applicable to the initial and intermediate steps in regulation of the North Sea. It is important to note, however, that our predictions of the results to be obtained with optimum fishing are based on the premise that all fleets will ultimately be using the same size of mesh. To achieve this, equivalent changes in fishing intensity and mesh size could not be used throughout the transition to optimum fishing, and eventually the fishing intensity of each fleet would need to be reduced by roughly the same proportion. In general, the use of more than one size of mesh on any one species would not produce results as good as the best single size, though if they were eumetrically suited to the species mainly fished by the fleets using them it would be possible to get even better results. This, of course, would amount to composite regulation, and it may well be that a natural evolution from uniform to composite regulation could take the form of regional modifications of mesh size based on the requirements of the main groups of fish and applied to the fleets specialising in them. In the meanwhile, the various methods of making reductions in fishing intensity provide considerable scope for each country to increase its profit margin by improvements in efficiency of vessels and gear and in the organisation of its fishing industry, while yet satisfying the criteria of equivalence.

Several proposals for regulating the North Sea demersal fisheries were put forward at the 1946 Overfishing Conference, the two most directly useful being that the total fishing effort should be decreased to 85% of its value during the years 1936-1938, and that the cod-end mesh size should be increased to 80 mm. The results of investigations described in this paper can be used to assess the long-term effects of these regulations with reference to pre-war conditions, on the basis that a decrease in total effort would decrease the fishing intensity on each species in roughly the same proportion.* In Fig. 20.9 we show the predicted changes in average yield of plaice, haddock, cod and sole plotted against fishing effort as a percentage of the mean pre-war level (in effect, the quantity "I" used in previous diagrams of this section). The curves for plaice and haddock are based on theoretical models whose properties have been examined in detail in §§17 and 18, while those for cod and sole are calculated using the parameter estimates given in §20.2.2. In comparing results for these four species it must be remembered that the same degree of reliability cannot be attached to those for cod and sole as for plaice and haddock. Nevertheless, the parameter values used for cod and sole would seem to be the best available at the present time and we believe them to be sufficient to establish the main features of the reaction of these two species to the two kinds of regulation proposed.

The continuous lines of each diagram are calculated with constant parameters, the lower referring to a 70 and the upper to an 80 mm. cod-end mesh of trawls (or to sizes of other gears giving equivalent selectivity). Thus reading along the curves from right to left shows the effect of decreasing fishing effort with a fixed mesh size of either 70 or 80 mm., while reading vertically shows the effect of this change of mesh with fishing effort constant. The combined effect of both a reduction to 85% of the pre-war fishing effort and an increase of mesh from 70 to 80 mm. is shown by the intercepts of the upper curves on the left hand axes. Comparing slopes of the curves of Fig. 20.9, therefore shows the degree of response of each species to a reduction in fishing effort, while the vertical distance apart of the 70 and 80 mm. curves shows the relative response of each to this increase in gear selectivity. The broken curves for plaice and haddock are those obtained with growth density dependent but recruitment constant†; they can therefore be regarded as showing

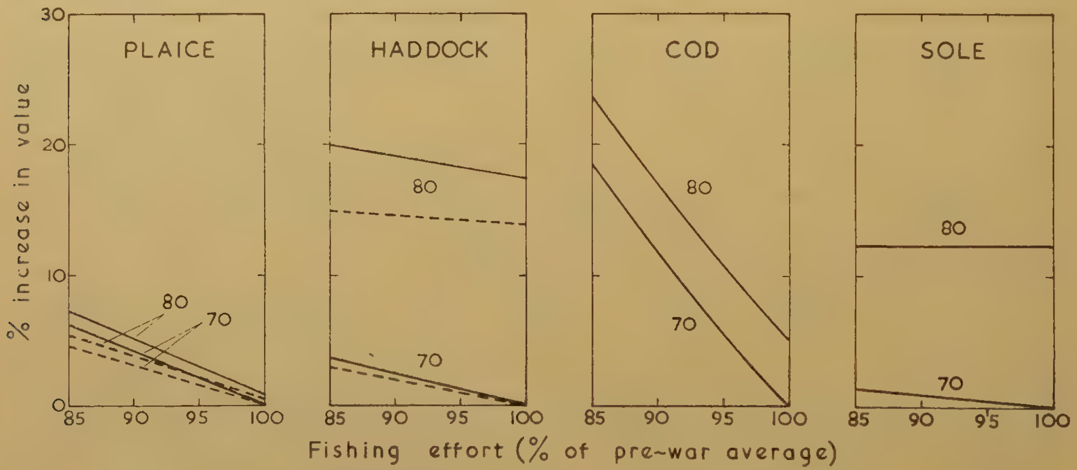

FIG. 20.9 PLAICE, HADDOCK, COD AND SOLE (SEPARATELY): EFFECTS OF REDUCTION TO 85% OF PRE-WAR FISHING EFFORT AND INCREASE IN MESH FROM 70 TO 80 MM.

[Ordinates show the estimated percentage increase in value, with abscissae giving fishing effort as a percentage of the mean pre-war level. Curves for 70 and 80 mm. meshes are labelled accordingly. Continuous lines are calculated with constant parameters; broken lines for plaice and haddock show probable effect of density dependent growth. Plaice and cod show the greater response to the reduction in fishing effort, haddock and sole to the increase in mesh.]

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* In April 1954, a minimum cod-end mesh of 75 mm. for trawl nets and 70 mm. for seine nets was adopted internationally for the North Sea and adjacent waters (see, e.g., Convention for the Regulation of the Meshes of Fishing Nets and the Size Limits of Fish, H.M.S.O., London, 1956; and Statutory Instruments, 1956 No. 1202, Sea Fisheries, H.M.S.O., London, 1956). The assessments given in this section do not refer specifically to this regulation, but its probable effects can be taken as roughly half those estimated here for an increase in trawl cod-end mesh from 70 mm. to 80 mm.

†For plaice, Fig. 18.9 shows that about 25% of the increase in yield going from $I = 1{\cdot}0$ to $I = 0{\cdot}85$ (i.e. from $F = 0.75$ to 0.62) calculated with constant parameters is lost when density dependent growth is introduced. For haddock about 20% of the increase calculated with constant parameters is lost when I is reduced from 1·0 to 0·85 (Fig. 18.10) and a similar correction must be applied to the effect of an increase in mesh from 70 to 80 mm. in this species (Fig. 18.12). The correction for a combined change to $I = 0{\cdot}85$ and a mesh of 80 mm. in this species is about 25%.

something like the minimum effect to be expected, since we concluded in §18.5.2 that a relatively slight increase of recruitment with egg-production would be sufficient in the long run to compensate for the slower growth.

The first point to note in Fig. 20.9 is that all the 70 mm. curves ascend to the left, showing that a decrease to 85% of the pre-war fishing effort with the 70 mm. mesh retained would cause the yield of each species to increase. The increase is greatest in cod and least in sole; in the latter species it is in fact so slight that for a conservative estimate it would probably be better to disregard it. The effect of an increase in mesh from 70 to 80 mm. is also beneficial in all four species, though it is much more marked for haddock and sole than for plaice and cod, even after allowing for density dependence. There are two reasons why this is so. One is the differences in shape and rate of growth; thus the large girth of plaice results in the mean selection length being increased by only two centimetres (from about 15 to 17 cm.), while the increase for cod (23 to 26 cm.) covers only a few weeks of life because of its rapid growth. The other is that neither plaice nor cod of the length concerned are fully represented in the main fishing areas, so that the potential effect of the mesh increase is correspondingly less. The evidence on this for plaice has been reviewed in §15.1.3; for cod we have constructed the 80 mm. curve by assuming that about half the fish of this range of length are exposed to the full fishing mortality (see §20.2.2)*. The outstanding impression gained from Fig. 20.9 is therefore that of the two proposed regulative measures the reduction in fishing effort would have the greater effect on yield of plaice and cod, while the increase in mesh size would benefit primarily the yield of haddock and sole. As a corollary, it can be seen that these two measures are not equivalent in terms of final benefit for any of the four species considered separately (see §19.3.2).

The effect of these regulative measures on the combined yield of the four species is shown in Fig. 20.10.1. This is constructed by adding the separate changes weighted according to their pre-war price indices given in §20.2. The heavy continuous lines refer, as before, to assessments using constant parameters and the thin continuous line for the 80 mm. mesh is that obtained by disregarding any effect in cod of increasing the mesh to 80 mm. The broken lines allow for density dependence and are based on assessments of this in plaice and haddock. It is now seen that each regulation causes about the same change in total value, of which a minimum estimate is 6%; hence in terms of combined value both measures are equivalent. Moreover, the effect of both measures together is now seen to be greater than either alone, a conservative estimate being an increase of about 10% in total value. Equally important are the changes in value per unit effort that would result, which are shown in Fig. 20.10.2. The much greater benefit in this respect of reducing fishing effort is apparent, and it is also seen that allowances for doubtful factors such as density dependence and the precise effect of the mesh increase in cod have a relatively smaller effect on changes in value per unit effort resulting from reduction of fishing effort than on value itself.

The steady state to which the stocks have returned since fishing was resumed in 1945 is broadly similar to pre-war conditions, although certain relevant differences may be noted. In plaice, for example, the mortality rate declined after 1951 to a figure some 15% lower than the pre-war value. This has led to a small increase in yield but a catch per unit effort some 20% greater than pre-war; from Fig. 20.9 it can be seen that these are just the results that would be predicted from theory. The reduction in fishing intensity responsible for these changes has probably been caused by economic factors and there is, of course, no guarantee that it will be permanent; nevertheless, it provides a direct proof of the benefit of reducing fishing intensity as a regulative measure. The yield of haddock appears to be somewhat below the pre-war level; this may yet turn out to be due to a lower level of recruit-

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*Most codling below about 25 cm. were probably rejected at sea before the war, and a legal size limit of 30 cm. was imposed in 1948. Hence the main effect of a mesh increase from 70 to 80 mm. is to increase the survival rate of undersized fish and hence to increase the number reaching the minimum landing size. This can be estimated as $e^{xFt} - 1$, where x is the fraction of the full fishing mortality F to which fish of this length are exposed, and t is the span of age between the 50% points of the two meshes. Taking $x = 0{\cdot}5$, $t = 0{\cdot}15$ years and $F = 0{\cdot}66$ for $I = 1{\cdot}0$, this gives an increased survival of 5·1% at $I = 1{\cdot}0$, 4·5% at $I = 0{\cdot}95$ and 4·3% at $I = 0{\cdot}85$. The 80 mm. curve for cod of Fig. 20.9 has been constructed using these figures.

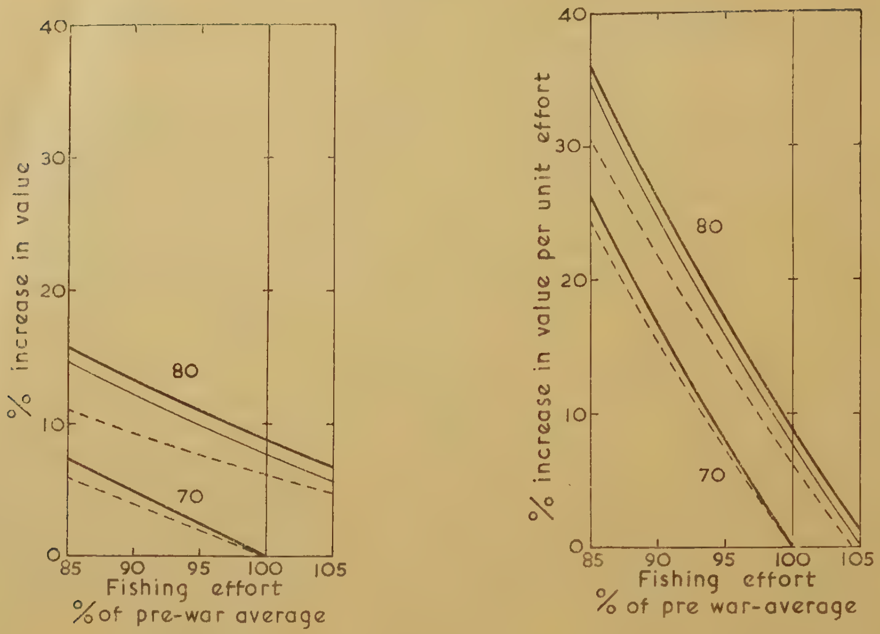

Fig. 20.10.1

Fig. 20.10.2

FIGS. 20.10 PLAICE, HADDOCK, COD AND SOLE (COMBINED): EFFECTS OF REDUCTION TO 85% OF PRE-WAR FISHING EFFORT AND INCREASE IN MESH FROM 70 TO 80 MM.

[Curves for 70 and 80 mm. meshes are labelled accordingly. As in Fig. 20.9 the continuous lines are calculated with constant parameters, the broken lines showing probable effect of density dependent growth. The thin continuous lines for the 80 mm. mesh are calculated on the assumption that the change in mesh will have no effect on the yield of cod.]

Fig. 20.10.1 Percentage change in combined value. The increase is virtually the same for either regulation alone and is greatest when both are introduced.

Fig. 20.10.2 Percentage change in combined value per unit effort. Note the much greater effect of the decrease in effort compared with the increase in mesh.

ment, but a contributory factor may be the increase in the minimum legal size limit for this species to 28 cm. that has been enforced in the United Kingdom since 1948. As this is near the upper limit of the selection range of a 70 mm. mesh it has probably increased the quantity of undersized fish rejected at sea. As a result, the benefit at the present time of increasing the mesh to 80 mm. for haddock may be rather greater than that shown in Fig. 20.9; it means also that the loss of yield during the transitional phase would be much less than that shown in Fig. 19.18, since the main effect would be to reduce the wastage of undersized fish, those above the size limit being little affected.

As far as can be judged without a more detailed investigation of post-war conditions, the effect of reducing fishing effort to 85% of its present level with a 70 mm. mesh in use would be similar to that shown in Figs. 20.10, conservative estimates being about a 6% increase in total value and a 25% increase in value per unit effort. The effect of increasing the mesh from 70 mm. to 80 mm. would probably be greater than before the war, possibly nearer 10% than 6% for both value and value per unit effort. It should be remembered, however, that these latter estimates assume that the total fishing effort remains stabilised; unless there is regulation to ensure this the natural tendency will be for fishing to increase as a result of the greater profit of fishing caused by the mesh increase (see §19.2.1.2). From Fig. 20.10.2 it can be seen that a 5% increase in fishing effort would be sufficient to eliminate the potential increase in value per unit effort caused by increasing the mesh to 80 mm. Although total value in these circumstances would still be some 5% higher than before the mesh increase (Fig. 20.10.1), economic conditions in the fishing industries would be virtually unchanged. With either kind of regulation (and especially with a mesh regulation) there may, of course, be some redistribution of effort towards those species showing the greatest response. Provided total effort is stabilised, however, the overall result would probably not differ much from that predicted on the basis of the relative fishing intensity on each species remaining constant (as in Figs. 20.10).

There is also the possibility that an increase in mesh size may cause the efficiency of the gear to increase a little. Although there is not yet sufficient information to estimate this effect with any precision (see §14.2), a change in mesh from 70 to 80 mm. could perhaps result in an increase of gear efficiency in the order of 5 to 10%, taking all species together. If it is supposed that total fleet size and fishing time remain stabilised at the pre-war level this would mean that the true fishing effort would also be increased by the same amount*, and the effect on the value of the yield can be gauged roughly from Fig. 20.10.1. Since the value curves fall rather slowly, the mesh increase would still be beneficial if accompanied by a change in efficiency of this amount, but the increase in value would be only some two-thirds to three-quarters of what it would have been had no change in efficiency occurred. Of course, if total fleet size or fishing time were reduced to compensate for the increase in gear efficiency, thus keeping the true fishing effort at its pre-war level, not only would the full benefit (in terms of value) be obtained from the mesh increase but the catch per unit fishing time would be correspondingly *increased.*

In the light of the requirements for optimum fishing of the North Sea demersal stocks summarised in §20.2.4, both a reduction to 85% of the present fishing effort and an increase in mesh to 80 mm. would therefore seem to be practicable and sufficiently cautious as first steps in regulation. The former would produce the greater economic benefits but even these are still much less than are potentially available from further reduction in fishing effort. Taking international prices and landings for 1951 as reference, the 10% increase in the combined value of plaice, haddock, cod and sole which we have put forward as a reasonably cautious estimate of the effect of the two regulations together for these species, would represent an additional income equivalent to about one and a half million pounds sterling a year, shared between the countries concerned. Furthermore, some benefit could reasonably be expected from the remaining North Sea demersal stocks, while the same regulations applied to the West coast hake fishery would probably bring the total extra income to well over two million pounds. If the objective of uniform regulation is adhered to and if, as we have suggested, optimum conditions may be obtained with a fishing effort less than half the pre-war level, it may turn out eventually that the need to maintain the yield of sole and whiting would not permit the size of mesh to be increased much above 80 mm. We would reiterate, however, that this is a matter which could scarcely be decided until the nations concerned had experienced the much more profitable fishing that would result from a substantial reduction in fishing intensity.

20.4 Conclusion

It seems, therefore, that even somewhat halting and imperfect steps towards the goal of more productive—and enormously more profitable—fishing cannot but be beneficial almost immediately. But any kind of regulation, however simple or limited, must inevitably involve the sacrifice, at some level, of part of the competitive element which characterises fishing as a means of utilising a natural resource, and its replacement by a measure of co-operation. In the early stages of regulation the obligation will fall primarily on the larger units within the fishing industries, and especially on the industries of each nation in their attitude towards one another's activities. Eventually, if regulation is to become perfected so that the maximum benefits are obtained, the greater will be the demand on the fisherman himself to bring about some modification of his individualistic and competitive approach to his problem of making a livelihood.

The final goal is too far away to make further speculation of this kind worthwhile at the end of an already long paper; but there is one point that is clearly within our province

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*The reader is reminded that fishing effort is defined in this paper as the product of fishing power (e.g. total fleet tonnage) and fishing time, *with gear of a standard efficiency*. If gear efficiency changes, it alters fishing effort correspondingly. In such circumstances the catch per unit effort does not have a direct economic significance, and it is necessary to refer specifically to the catch per unit fishing time (see §§3.3 and 19.2.2.1).

to anticipate, namely the improvement in commercial fishing statistics and in research sampling and investigations of the fish stocks that any substantial progress in regulation will call for. Despite all care in making predictions, steps in regulation will be experimental to this degree: that while the early ones cannot fail to be beneficial, the closer the optimum is approached the more accurately will the next step need to be predicted and hence the greater will be the demand on the information required. Yet it is the changes produced in the fisheries by the regulations themselves, whether they be the first or the last in the series leading towards the optimum, that provide the opportunity of obtaining, by research, just the information that may have been lacking previously. Thus the approach towards optimum fishing, and the increase in knowledge of where the optimum lies, can be two simultaneous and complementary advances; the benefits to the fisheries of such progress can hardly be exaggerated.

RESUMÉ

In our introduction (§1) we run briefly over the history of methods of attack on the problem of the best use of fish stocks under stress of fishing, that is, which have reached a state when their abundance is determined to a significant degree by the fishing activity. The method of this paper has been to set up mathematical models to represent the interaction of factors governing the annual yield of a fishery, and also the abundance of the stock, on which depends the catch per unit fishing effort. The yield and the catch per unit effort are, respectively, the bionomic determinants of the magnitude of a fishery and its profitability.

The four primary processes to be considered (§2) are: recruitment, growth, capture, and 'natural' death, that is, death from causes other than fishing. These processes, or factors, tend to change the total weight of the fishable stock, but in a stable fishery the nett result of their combined action determines the yield that can be taken year after year without changing the level of the stock. However, the magnitude of each factor depends, to a greater or lesser extent, on those of the others, and in developing the theory of fishing our method has been to represent the action of each factor by one or more parameters that can in the first instance be assumed to be constant and independent. A later stage is to extend the theory to allow for likely variations in these parameters and for interaction between the factors.

In §3 the four primary factors are formulated mathematically in the simplest way compatible with general observation. For recruitment, a distinction is made between the number of fish entering the exploited area and the number that survive to become liable to capture by the fishing gear in use. The average age at which the second stage is reached depends on properties of the gear, including, in trawls, the size of the mesh. Natural mortality is taken to be due to a number of causes acting independently, and so can be represented as an exponential coefficient. For convenience, the natural life of a fish is assumed to terminate abruptly at a certain high age, rather than to be of infinite duration. Fishing power is defined as the effectiveness of a vessel relative to that of a standard vessel; fishing effort as the sum of the products of fishing power and time spent fishing by each vessel in a year; and fishing intensity as fishing effort per unit area. Assuming, in the first instance, random encounters between gear and fish, mortality from fishing will cause the number of fish to decrease exponentially, as with natural mortality, and can be expressed by a coefficient that is directly proportional to fishing intensity. Departures from this simple form are considered at a later stage. To introduce the factor of growth it was necessary to express the relation between size and age of individual fish in a mathematical form, and one derived from von Bertalanffy's law of organic growth proved suitable. This expresses growth as the nett result of anabolic and catabolic processes which are themselves functions of the size of the animal.

The primary factors are brought together in §4.1 by considering a year-class of recruits to the fished area and applying the other three factors, represented in the appropriate mathematical forms, to deduce what the total yield from the year-class would be throughout its life in the fishery. By a simple transposition, this is shown to be the same as the yield in one year from all the year-classes present in a steady fishery, that is, one in which the biomass, or weight of stock, tends to remain at a constant level. Equation (4.4) expresses yield in this steady state in terms of the four primary factors. When the fishing mortality coefficient is taken as the independent variable, and the yield per recruit the dependent, we obtain a graph like that for plaice shown in Fig. 17.2, p. 312. When the mesh of net is the independent variable, the changes in the resulting magnitude of yield per recruit are of the form shown by the graph in Fig. 17.8, p. 316. Equation (4.4) refers to what we have called the 'simple model', and from this model are also derived (§5) expressions for yield in number, catch per unit effort, population number, population biomass, and mean length, weight and age of fish in the population and in the catch, all of which are needed in a full analysis and interpretation of fishery dynamics.

In Part II, we turn to the problems presented by change in the primary parameters, which are assumed in Part I to remain constant. In reality, we expect them to change, at least in some degree, and especially with changes in population density. We investigate, by elaborating the simple model, the effect of changing each in turn, keeping the others constant, preparatory to investigating the effect of changing all together.

Although in most marine fish populations—but perhaps not in all—recruitment appears to be independent of stock density, this cannot always be so, for example, when the number of spawning fish is extremely small. Instead of ignoring any such effect, it seemed better to develop a mathematical model incorporating a relationship between egg-production and recruitment which would be undetectable at sufficiently high levels of stock density. In §6 a simple balance is constructed by making egg-production proportional to the adult stock weight and the pre-recruit mortality coefficient a linear function of the density of young fish. The resulting model is offered as suitable at least until more is known of the actual course of events between the egg-stage and the stage of first becoming fishable. Egg-production and subsequent recruitment are related as in equation (6.10). Since egg-production is related to biomass, it is possible to eliminate recruitment from the simple model and obtain equation (6.23), in which the yield is given in terms of fecundity and pre-recruit mortality as well as of the factors formerly considered, namely those operating within the fishable life-span. We also demonstrate (§6.2) that, in a stock where recruitment fluctuates annually—as is common experience—the mean recruitment can legitimately be used instead of the actual to predict the average yield over a period; and we derive a model relating the variation of annual yield to the variation of recruitment, which is used later as the basis of a method of testing whether a regulated fishery is behaving in the way expected.

We next (§7) discuss variation in the natural mortality rate with age, for which there is some evidence for using a linear regression, and also the possible ways of testing the fishable life-span. We then develop an approximate method of expressing dependence of the natural mortality rate on adult stock density. Given the necessary information from two substantially different levels of population abundance, a comparatively simple method is shown for obtaining an equivalent constant natural mortality coefficient that takes account of a real variation with stock density.

Variation of the fishing mortality coefficient with age (§8.1) necessitates investigation of a more precise treatment of mesh selection, which we have hitherto treated as 'knife-edge', that is, escape of all fish up to a certain length and thereafter complete retention. Changes in ability to avoid the net as the fish grow larger and stronger can be treated on similar lines. Variation of the fishing mortality coefficient with age can also arise if two or more fleets fishing the same stock are using different meshes, and a model is developed for computing the total yield in these circumstances and also the yield to each of the competing fleets.

In practice, there are important periods when fisheries are not in a steady state, but are undergoing change due to changes in intensity of fishing or in gear selectivity. The effects of such changes have to be examined year by year, and in §8.2 we develop methods for dealing with such 'transitional' periods, which are used later for predicting the immediate effect of introducing a regulative measure as opposed to the long-term result when the new steady state is reached. In §8.3 we re-examine the simple relationship we have used between fishing intensity and fishing mortality, and show various conditions that require adjustments, as when fish and fishing are not uniformly spread over an area, and when searching or gear saturation are important. We also consider the important case of seasonal variation in fishing intensity, in the extreme form of a restricted fishing season, and show how the theory for a continuous fishery needs to be modified.

The growth of fish is known to be variable and to depend on the food supply, so there are several ways in which growth rate may depart from the form represented by von Bertalanffy's equation with constant parameters, which was used in constructing the simple model. In §9.1 we consider some other equations that have been used to express growth. We find them, in one way or another, inferior to von Bertalanffy's; but in certain circumstances a simple polynomial might be appropriate. Parameters of the growth equation may also vary with age (§9.2)—there might be a break in the growth pattern at recruitment or at maturity—and we show how we would deal with that phenomenon. Differences in the rate of growth between individual fish would probably be of little consequence if it were not for the fact that there is usually some form of 'size threshold' for entry of fish to the exploited area or catch. This results in the largest members of a year-class entering first, and it may take several years before the whole year-class is recruited, depending on the range of variation in pre-recruit growth (§9.3). We suggest that this phenomenon can be dealt with by calculating the yield separately from each 'sub-group' of recruits that comes into the fishery, taking its particular rate of growth into account.

The most important cause of variation in growth lies in its dependence on food consumption, the evidence being that this can often outweigh all other causes. We treat this problem (§9.4) mainly by analysis of the interaction between the fish population and its food supply, including the dynamics of the populations of food organisms. We consider that the available evidence leads to the conclusion that the principal effect of varying food supply is on the anabolic component of metabolism rather than on the catabolic, since the former must be directly dependent on the rate of food consumption. The evidence also seems to define the lower limit of growth rate possible without the fish being killed as nil—when the food supply is just sufficient for maintenance purposes only—and the upper as that achieved when fish are eating to full capacity. Where data are available on growth-rate at various levels of population density it is a comparatively simple matter to determine the required anabolic parameter at each level, and so derive some simple law relating growth and biomass. An example would be an inverse linear relationship, and this we do in fact find useful in our study of plaice and haddock.

Just as we have considered the effects of fishing on biomass and yield of a population of fish, so we now consider the effects of predation by fish on the biomass and yield (as supply of food for fish) of a population of food organisms. However, the yield obtained by a given amount of fishing depends on the abundance of the fish population, whereas the amount of food eaten by that fish population can be calculated if its abundance and rate of growth are known. The first step, therefore, is to derive an expression for the total food consumption of a population of fish growing at a specified rate. First an expression for the maintenance requirements in terms of body weight is derived, using experimental data; then, assuming that efficiency of utilisation of food is constant, an expression is found for the food required to produce the total annual weight increment due to growth in an observed population of fish. Kostitzin, however, and others have formulated expressions for the variation of efficiency of utilisation with the amount of food consumed, and we adopt his equation for our purpose, thus arriving at equations for actual and maximal food consumption of a fish population in terms of its abundance, age-composition and growth rate.

We next have to consider how the food consumption will vary with the availability of the food. Here the absence of significant and satisfactory information makes it necessary to consider several possible hypotheses. The most realistic of these takes account of grazing power, relating this to body weight and hunger of the fish, and of the effect of grazing by the fish population on the productivity of the food species. The parameters of this model can, however, be estimated if two levels of stock density and corresponding growth rates are known, together with the physiological data mentioned above, and it is used in §18.4 to investigate the relation between growth and density of plaice. Consideration of the effects introduced by predation on two or more food species leads to a review of the methods of reporting food preference and vulnerability, two factors which can rarely be separated in the field. According to our equations, as a fish population decreases in abundance a relatively smaller proportion of the less preferred or less vulnerable foods will be eaten, which is in accordance with observation. From the degree of aggregation of the food organisms, effects are foreseen on both vulnerability and efficiency of utilisation that might be of some importance. A method is developed for evaluating the effect of direct destruction of food organisms by the trawl, if this proved important.

The next complication to be investigated (§10) is that of lack of uniformity in the spatial distribution of fish or of fishing effort, involving an analysis of the movement of fish within the exploited area. The solution proposed is to divide an area into sub-areas small enough for the effects of any aggregation of fish or fishing units within them to be disregarded, and to express movement of fish between sub-areas by transport coefficients, which are simpler parameters than diffusion coefficients, although both are derived by analogy with the kinetic theory of gases. Equations are derived for the yield from the whole area made up of such sub-areas, which are applicable to many of the cases encountered in practice. When fish and fishing are unevenly distributed the total fishing effort is no longer proportional to the fishing mortality coefficient as estimated from catch samples, but a measure that is proportional can nevertheless be computed. This is called the effective overall fishing intensity, and is the sum of the fishing intensities in each sub-area weighted by the density of fish in each. It can readily be computed for the past from appropriate commercial statistics, but the future prediction of how the fishing mortality will be altered by a change in total effort or, more particularly, in its distribution, is more difficult unless the pattern of fish dispersion is known in some detail. Certain simple cases are considered, however, which may be useful in establishing the limits within which the true answer will lie. A further use of transport coefficients is in a formulation of migration as 'orientated dispersion'. Somewhat similar concepts lead to the beginnings of a theory of fleet deployment in relation to the distribution of the fish stock. It is clear that there is an optimum proportion of time spent in searching, as distinct from fishing, depending on the form and degree of aggregation of the fish.

The methods so far developed, for populations of single species of fish, are applicable with appropriate modification to fisheries based on several species that are caught together by the same gear (§11). Where the species can be considered as independent of each other, each can be treated separately and as subject to its characteristic intensity of fishing, taking note of any changes indicated by suitable statistics. Certain cases of interdependent fish stocks are also amenable to simple treatment. When two species compete for a common food supply, the effects can be formulated provided there are data for two levels of stock density for which the usual parameters are known. As a result of the analysis an improved index of competition is proposed. Also, a model is developed for calculating the yield from each of two fish populations when one is a predator of the other, which allows the effect on both of changing fishing intensity or mesh size to be predicted. When dependence of recruitment on stock density is introduced into this model, we approach a special theory of a predator-prey system; a general theory we regard as premature and possibly illusory, owing to the possibility of so many special cases that may entirely alter the dynamic properties of the system.

For most of the theoretical methods developed in this paper, data are available to which they can be applied. We find these for plaice and for haddock of the North Sea, and occasionally we turn to other species elsewhere. Because the data were not always collected specifically to the mathematical requirements, there are many gaps and imperfections, but nearly always we have found them in the main adequate. The estimation of parameters from those data is the subject of Part III of our paper.

Since fish population data come largely from catch samples, a necessary preliminary (§12) is an analysis of the fishing power of the commercial vessels responsible for some of the most important characteristics of the fish populations that we investigate, and which may also provide the catches that are sampled (as in plaice). Fishing 'power factors' were obtained for a large number of trawlers by comparing their recorded catches per unit effort for each trip in each of six statistical rectangles of the southern North Sea; by means of direct and indirect comparisons an average power factor was estimated for each ship, relative to one as a standard. The power factors for steam trawlers were roughly proportional to gross tonnage, but were log-normally distributed within each tonnage class (Fig. 12.1, p. 175). The geometric means of the power factors for each tonnage class were therefore plotted against tonnage (Fig. 12.2, p. 175); the data were fitted satisfactorily by the proportional equation $P.F. = 0{\cdot}0073\times$ gross tonnage. For motor trawlers, the equation was $P.F. = 0{\cdot}0102 \times$ gross tonnage, so that ton for ton a motor trawler has a fishing power some 30% greater than a steam trawler. An alternative index of fishing power for motor trawlers was found to be brake horse power, the equation being $P.F. = 0{\cdot}0047 \times$ brake horse power. A check was obtained from a comparative fishing experiment using the steam trawler SIR LANCELOT and the motor trawler PLATESSA. From this analysis we suggest that a steam trawler ton-hour would be suitable as a basic unit of standardised fishing effort, and the same per square mile as an index of intensity. While this index needs to be used with care and must be adjusted for improvements in efficiency of gear or vessels, it would undoubtedly increase the usefulness of commercial statistics, especially in the North Sea where so many different kinds of vessels and gears are used.

Estimates of the total mortality coefficient $(F + M)$ can be made from an index of abundance (i.e. catch per unit effort) of one year-class in successive years of observation, or, less reliably, from relative abundance of age-groups averaged over a period, but both methods have to neglect any change in total mortality, and other sources of bias have to be guarded against. In the North Sea during the inter-war sampling periods, the figure found for plaice is 0·83, for haddock 1.2 (§13). The age at the end of the life-span is taken as 15 years for plaice and 10 years for haddock, but the exact values are not important.

Turning to methods of obtaining separate estimates of fishing and natural mortality we treat first the use of returns from marking experiments, these forming an example of the 'ratio' methods, as distinct from 'enumeration' and 'index' census methods, to which we give references in the literature (§14.1). We find that two earlier methods of estimating the fishing mortality coefficient F are erroneous, although one of them gave a substantially correct result owing to peculiarities in treatment of the data used. A simple method for estimating F clear of the rate of shedding of marks and other error (the 'other loss' rate X) is given for the case when there is no sudden mortality or other abnormal events at or soon after the time of liberation, and when the fishing intensity and other-loss rate can be taken as constant over the whole recapture period. If the fishing intensity varies in an unknown way it is possible to minimise the effect by grouping recaptures from a number of separate liberations into equal periods at liberty. If the variation in fishing intensity is known, however, it may be possible to use methods for estimating F and X that do not require a knowledge of the number of fish liberated, thus avoiding errors due to marking mortality and also those that could otherwise be caused by incomplete reporting of recaptures. Age or size-groups of marked fish can, if necessary, be treated as separate experimental batches. Spatial variation in fishing effort may well be important in marking experiments; one way of dealing with this is to estimate the relation between F and fishing intensity for the marking area, and then compute the effective overall fishing intensity on the whole population by methods developed in earlier parts of this paper. It is valuable in some instances to use continuous marking and recapture, for example, when fish have to be marked by fin-clipping and a particular fish cannot be recognised on recapture; a method of estimating F is shown for this kind of experiment. More complex, but still practicable, methods are derived for estimating the rate of shedding of marks from experiments with two marks attached to each fish. Methods are given for determining transport coefficients from marking experiments, and dispersion coefficients when all the marked fish are liberated at one point.

Examples of the application of some of these methods are given in §14.1.3 in a preliminary analysis of the post-war plaice marking experiments, in which there were between one and two thousand recaptures. The majority of fish were liberated in six of the most heavily fished rectangles of the Southern North Sea, and in these the average value of F was estimated as about 1·5. Since each was fished with an average of 6,000 steam trawler ton-hours per square mile per year, an estimate of 0·25 was obtained for the constant c, relating fishing mortality to fishing intensity (in units of a thousand ton-hours per square mile). The other-loss rate in these experiments was high, in the order of 10, but analysis of dispersion of marked fish from the marking area showed that this factor was responsible for the greater part, but not all, of the other-loss rate. A double-marking experiment was also carried out, showing that the rate of shedding of marks was probably between about 0·2 and 0·4. The magnitude of these dispersion and shedding rates prevented any estimate of the true natural mortality coefficient being obtained from the marking experiments alone.

The next subject considered is the variation of the fishing mortality coefficient with age as a result of mesh selection (§14.2). Various experimental methods are compared and it is concluded that, in general, the alternate or parallel haul technique with different sized meshes is likely to give the most reliable results. Plaice experiments of this kind are analysed and it is shown that a closely proportional relation exists between the 50% selection length and mesh size (gauge width), the factor being 2·2. For haddock, the commercial experiment carried out by Davis was examined; in this case the two mesh sizes differed little and their selection ranges overlapped, but a method for estimating the true selection factor is devised, giving the estimate 3·3. It is shown that these selection factors for plaice and haddock could be predicted fairly accurately from a knowledge of the maximum cross-sectional area of the fish in relation to the dimensions of the mesh lumen. Factors responsible for the spread of a mesh selection ogive are also considered; of these, the two that can be measured independently—the variation of mesh size within the cod-end and the variation of length of fish at a given girth—are shown to account for about 30% of the spread of the plaice ogives. The section is concluded with a note on the theory of estimating the overall mesh selectivity of a net, i.e. including escape through meshes other than the cod-end.

Having previously dealt with the estimation of the total mortality coefficient ($F + M$) from age-composition data, we now turn to methods of estimating the two coefficients separately from data of this kind (§14.3). The essential requirement is that F should have varied in a known way during the period covered by the data; either in the population as a whole as a result of known changes of fishing effort, or with age of fish through gear selectivity. The basis of the method is then to compare the changes in ($F + M$) that result from particular changes in fishing intensity, or gear selectivity with age; the more nearly these changes are in proportion the smaller must be M, and vice-versa. It is shown, in fact, that F and fishing intensity are linearly related, and this is used to estimate F and M separately. Attempts to apply the method to pre-war plaice and haddock data fail because the change in effort was so small that it did not produce measurable changes in ($F + M$). Examples of its successful application to three other fisheries are, however, given.

At this stage there is still the problem of obtaining an estimate of the natural mortality coefficient M in plaice and haddock. The factor relating fishing mortality to fishing intensity estimated from the plaice marking experiments ($c = 0{\cdot}25$) is used to compute the effective overall value of F for the whole population from the distribution of commercial catch and effort. It is found that the greater part of the total mortality coefficient estimated from catch samples can be accounted for in this way, and that M is, therefore, small relative to F, but the absence of detailed commercial statistics from other countries fishing North Sea plaice prevents an accurate estimate of M being obtained. However, it was found possible to compare the abundances of certain year-classes of plaice that were sampled representatively both in 1938-1939 and again in 1945-1946. Since there was little, if any, fishing in the main plaice area of the North Sea during this period, the decrease in abundance of the year-classes during this time gives a direct estimate of the average natural mortality coefficient during the war period. This was found to be about 0·1 (in annual units), so that the value of ($F + M$) of 0·83 for the pre-war period is taken as being made up of an $F = 0{\cdot}73$ and an $M = 0{\cdot}1$. This method could not be used for haddock and, indeed, an accurate estimate of M for this species is still lacking. However, from a consideration of the age-composition data obtained by research vessel sampling with small-meshed gear it is concluded that M may not be much greater than 0·2. Provisionally, this is the value adopted for haddock, so that for the pre-war period the average value of F is taken as 1·0, since ($F + M$) was found earlier to be about 1·2.

§15 deals with estimation of recruitment parameters: the mechanism and average age of recruitment, the average annual number of recruits, and fluctuations in annual recruitment in relation to causal factors and their effect on fluctuations in the annual yield. A special feature of the North Sea plaice population is that recruitment consists of an off-shore movement to the main fishing area from the nursery grounds on the eastern side of the North Sea. This movement is analysed in detail in §15.1 using data from the research vessel sampling of the Leman-Haaks line of stations carried out for a number of years prior to 1930. It is shown that the off-shore movement follows the law of random diffusion, which lends support to the use of this law as the basis of our earlier theory of fish movement. The dispersion rate was found to be such that, on the average, a fish at the end of a day would be about a mile away from its starting point, a figure which is in reasonable agreement with the dispersion rate estimated from marking experiments. Total mortality rates calculated for the pre-recruit age-groups from the same data indicate that the average age at recruitment to the exploited phase is somewhere in the fourth year of life, but a more accurate estimate was obtained by observing the pattern of entry of recruits into the commercial catch from market samples. This showed that about nine-tenths of the recruits are in age-groups III and IV, the remainder being in age-groups II and V; the average age at recruitment (i.e. the parameter $t_{\rho'}$ in the yield equation) was estimated as 3·7 years. The average recruitment over a period can be estimated in terms of actual numbers quite simply if growth and mortality rates are known, by dividing the average annual yield by the yield per recruit predicted from the yield equation (4.4). For the inter-war sampling periods this number was found to be 250 million plaice and 850 million haddock (§15.2). Other population characteristics can readily be computed from theoretical models when the absolute recruitment is known; for example, the average number of plaice in the fishable stock of the North Sea for the same period was about 350 million. From a knowledge of the plaice recruitment in each of the pre-war sampling years the variance of the annual recruitment was calculated and used to predict the variance of the annual yield, on the assumption that recruitment fluctuation was the only cause of yield fluctuation. The predicted variance of yield was found, however, to be about 25% greater than the observed variance; it is shown that this discrepancy is probably caused by observational errors in the recruit estimates—a cause of variation which does not, of course, apply to the yield statistics, or, at least, not to a significant degree. In this way the coefficient of variation of the plaice age-composition data due to observational error (mainly sampling error) was estimated as 27%, a figure in good agreement with that obtained from recent investigations on the sampling process itself. The predicted variance of yield in haddock was, however, found to be some five times greater than the observed variance, suggesting a larger observational error in the age-composition data.

Attempts to find a relation between egg-production and recruitment in plaice are inconclusive, but there is some indication of one in haddock. For later studies on the effect of introducing the dependence of recruitment on egg-production in theoretical models, a range of values of the parameters α and β of equation (6.10) are deduced which are not incompatible with the haddock data. This leads to a discussion of the general problem of relating recruitment fluctuations to causal factors, and it is stressed that no one factor alone can be expected to give a high correlation—if only because of the sampling variation in the recruit estimates. The subject of recruitment is concluded by a review of the relationships between egg-production and recruitment that have been found in certain other species.

The subject of §16 is the estimation of growth parameters and the dependence of growth on population density and food supply. First it is necessary to determine the relation between weight and length (§16.1), and in both plaice and haddock this is found to be described sufficiently well by a simple cubic equation. It is pointed out, in this connection, that attempting to improve on the fit to data by using the allometric weight-length formula means abandoning the simple dimensional relationship between these two variables and introduces considerable theoretical difficulties. A method of fitting the von Bertalanffy growth equation, and hence of estimating the parameters it contains, to weight or length data is illustrated for plaice and haddock in §16.2; it is shown also that the equation describes well the growth of two other North Sea species, cod and sole, which differ greatly in their rate of growth. When fitting the von Bertalanffy equation to plaice it is found that the weight of the youngest age-groups in catch samples is greater than would be expected, due to the fact that fish of these age-groups are wholly or partially recruits which are the fastest growing members of their year-class. The phenomenon is treated in §16.3 in more detail, the average weight of fish in each recruit sub-group being estimated with the help of certain hypotheses concerning the relation between pre-and post-recruit growth rates.

The method of establishing an empirical relation between growth and density depends on whether the data available refer to steady states or to annual fluctuations in these two characteristics (§16.4.1). The plaice provides an example of the former kind of data, and by comparing the growth during the pre-war steady state to that during the war period when the density is estimated as being at least three times greater on the average, a well-marked effect is found. The year to year fluctuations in haddock density during the pre-war period were large enough to produce measurable changes in growth (as measured by the value of the parameter L_∞ for each year), but it is shown that the relation obtained by plotting contemporary values of L_∞ and density may underestimate the true relation in a steady state because of a time lag between changes in density of fish and of the food organisms. For some of the haddock data it can, in fact, be demonstrated that although the growth rate in a particular year is dependent mainly on the density of fish in the same year, the density during the preceding year also makes a significant contribution. When all the data are used the effect is, however, no longer significant and it is not necessary to take account of it in deriving the relation between growth and density for steady states. The relation between L_∞ and population number-density in haddock is found to be closely linear, which is in harmony with predictions from theoretical models described in §18.4 and gives some basis for using a similar kind of relationship for plaice where there are only two pairs of observations of growth and density. The dependence of growth on feeding and food supply can be examined in plaice only (§16.4.2), and even here it is necessary to rely entirely on the experiments carried out by Dawes. Although these have limitations for the purpose we require, they give consistent results and enable working estimates to be obtained for all the necessary parameters. The maintenance food coefficient and an average estimate of the efficiency of food utilisation are determined first; it is found the maintenance food requirements are almost exactly proportional to the two-third power of body weight, and that the efficiency of utilisation of *Mytilus* flesh for growth is about 0·2. A more detailed analysis is then made of the variation of utilisation efficiency with the amount of food consumed; Kostitzin's equation is used for this purpose, and is satisfactory within the limits of the data. From the rate of growth of experimental fish supplied with as much food as they could eat, the order of magnitude of the limiting growth parameter, $W_{\infty L}$, is established; it is some five or six times the value of W_∞ found for plaice in the North Sea.

Part IV of our paper describes the properties of the various theoretical models developed previously, using parameter values estimated in Part III for plaice and haddock. The simple models of Part I are considered first in §17, and their properties are taken as a basis for examining the modifications caused by introducing the more complex inter-relations in the models of Part II. The two main variables are the fishing mortality coefficient F (determined by the fishing intensity) and the age $t_{\rho'}$ at which fish enter the exploited phase (dependent on the gear selectivity). In the first instance each of these in turn is kept constant, at the value estimated for the pre-war period, and equation (4.4) is used to calculate the steady yields corresponding to a range of values of the other—above and below its pre-war value. These are shown graphically, and it is found that both the curve of yield against F and that of yield against $t_{\rho'}$ have a maximum, that of the former occurring at a value of F about a quarter (0·22) of the pre-war value (0·73). The maximum of the yield—$t_{\rho'}$ curve is at a value of $t_{\rho'}$ corresponding to a mesh considerably larger than the one then in use (70 mm.). At this point, therefore, the conclusion from the simple models is that a greater steady yield of plaice could be obtained with either a lower fishing intensity or a larger mesh size than applied during the pre-war period. The same is true for haddock, although here neither the potential increases in yield, nor the changes of F and $t_{\rho'}$ from their pre-war values that are needed to produce these increases, are as large as in plaice. Attention is then turned to the effect on steady yield of changes in both F and $t_{\rho'}$ together. To show this, F and $t_{\rho'}$ are made the co-ordinates of a graph in which yield is plotted in contours; each yield contour specifies all possible combinations of F and $t_{\rho'}$ that together would produce the yield in question. This kind of graph is called a yield-isopleth diagram, and it shows that an even greater steady yield of both plaice and haddock could be obtained by adjustment of both F and $t_{\rho'}$ than by changing either alone. The yield-isopleth diagram is used as the basis of a discussion of fishery regulation in §19. In addition to yield, the variation of other characteristics of the population and catch with F and $t_{\rho'}$ are examined, including population biomass, numbers, and the average size and age of fish in the catch. While dealing with simple models, opportunity is also taken of investigating the effect on plaice yield curves of different values for certain parameters, including in particular the natural mortality coefficient M and the maximum age t_λ. It is shown for plaice that values of the latter higher than we have taken (15 years) make little difference except at very low values of F, but that yield curves are much more sensitive to alterations in the value of M. The general picture is not, however, altered much with M 50% greater or smaller than the estimate we have used (0·1), but putting M as high as 0·5 completely removes the maximum in the yield-fishing intensity curve.

The properties of the more complex models developed in Part II are examined in §18, starting by treating each extension of the simple theory in turn and later combining certain of them in one model. Some are found to produce little difference in the shape of yield curves compared with the use of the simpler approximation, at least within the range that need be considered in practice. This is true for the more exact representation of a mesh selection ogive (§18.1) and for treatment of recruitment occurring in several age-groups with each recruit sub-group having a different rate of growth throughout life (§18.3). Introducing the variation of parameters with population density can, however, cause important differences. We have as yet no evidence whether the natural mortality rate in either plaice or haddock is density dependent, but by working on the assumption that M, if it changes at all, increases linearly with density, it is possible to establish what may be regarded as a fairly extreme case (§18.2). Yield curves incorporating this relation have lower maxima than those with a constant natural mortality rate and these occur nearer to the pre-war values of F and $t_{\rho'}$.

The effects of the density dependence of growth are examined in two main ways (§18.4). One is to use the empirical linear relationships derived from the analysis of plaice and haddock data in §16; the other is to use the growth and feeding data for plaice in theoretical models that take account of the interaction between a fish population and the food species on which it lives. The most realistic of these, in which the dynamics of the food populations are introduced, is found to produce yield curves very similar to those obtained with the linear relationship, and it is concluded that the latter is likely to give, in general, reasonably satisfactory assessments of the effects of density dependent growth. The yield $-F$ curve with growth density dependent differs from that with a constant growth in a way qualitatively similar to the difference between curves with constant and density dependent natural mortality, the peak being less marked and at a higher value of F. The effect of an increase in mesh size with growth density dependent is perhaps the most interesting. The immediate effect is to cause fish to enter the exploited phase at a larger size than before, and hence at a higher age; but the increase in density resulting from the more abundant pre-exploited phase slows the growth. This means that fish take even longer to grow to the selection point of the new mesh, which in turn causes the density to increase still further, and so on. The resulting yield curve may differ very much from that calculated with a constant growth.

The effects of dependence of recruitment on stock size are examined by means of self-regenerating models incorporating the relation between egg-production and recruitment defined by equation (6.10). The changes in population size that are found to result from quite small alterations in fishing mortality or mesh size from their pre-war values are so large with recruitment alone density dependent that it is clear that, in practice, compensatory changes in some other factors would certainly occur; this is taken into account by constructing a model in which both recruitment and growth are simultaneously density dependent (§18.5). It is found, nevertheless, that within limits the changes in recruitment can outweigh those in growth and cause yield curves to have higher maxima than if all factors are treated as independent of density. These models have another property not found previously, namely that, depending on the extent to which recruitment is made to vary with egg-production, at certain high values of F and small meshes the population becomes extinct because the egg-production is too small to maintain recruitment.

The last problems to be examined (§18.5) are the consequences of fishing being restricted to a part only of the area occupied by the fish population, using certain of the models developed in §10. The plaice is taken for purposes of illustration and a uniform rate of dispersion is postulated of the order of magnitude found from the marking experiments analysed in §14. A series of yield curves is then constructed, with fishing restricted to various fractions of the whole area. It is found that with up to about a quarter of the area unfished the yield curves are little affected, but with further restriction of the fishing area the maximum becomes less marked and occurs at progressively higher values of F. This is the kind of yield curve that might apply to a coastal or 'fringe' fishery, where the main bulk of the population is unfished and acts as a reserve to make good the depletion in the fishing area.

§18 is concluded by a review of our findings so far for plaice and haddock. The conclusion reached in §17 from the properties of the simple models, namely that in both species a greater steady yield could be obtained with less fishing or a larger mesh size than applied in the pre-war period, is still true, but nearly all the more complex interactions studied in §18 suggest that the actual changes required in fishing intensity and, especially, in mesh size are not as great as would be predicted from the simple models. It is shown also that the general properties of the plaice and haddock yield curves provide a reasonable and consistent interpretation of the course of events in these fisheries since the later years of the last century, namely an initially rapid expansion of the fleets which gradually slowed down as the fish resources became unable to meet the demands of the increasing fishing effort, stability eventually being reached when the profit in fishing was no longer sufficient to support any further expansion. In this condition the industries are operating at something approaching the minimum profit level, with its associated economic implications, and it is impossible to avoid the conclusion that some form of regulation is needed to bring any improvement. This is the subject of the next section.

§19 is concerned with the general principles and methods of fishery regulation. Within its biological framework this is essentially an economic and social problem, conditioned by the fact that a prime motive in any commercial fishery is to obtain the maximum income, in the form of yield, that is possible with a given expenditure in fishing. Since the costs involved in using gears of various selectivities (e.g. mesh sizes) are usually little, if at all, different, we suggest that one aim should be to adjust the gear selectivity so that it enables the greatest yield to be obtained with each particular amount of fishing; this is called *eumetric fishing*. The generalised yield curve is, therefore, that relating steady yield to fishing intensity with the mesh size varying throughout to produce eumetric fishing. It is shown how these eumetric yield curves can be constructed from yield-isopleth diagrams, and examples are given for plaice and haddock with parameters both constant and density dependent (§19.1). The general shape (though not the location) of eumetric yield curves for a single species is found always to be same. As the fishing intensity is increased the yield also increases but to a progressively lesser extent and without passing through a maximum; eventually, as the fishing intensity becomes infinitely high, the yield approaches a limiting value, which is the greatest possible steady yield that could be obtained from the fishery. It follows that with eumetric fishing the conventional idea of fishery regulation—to adjust the amount of fishing so that the maximum steady yield is obtained—must be abandoned; the greatest possible yield can be obtained only with an infinitely high fishing intensity and hence at a prohibitive cost. The question of deciding at which point on a eumetric yield curve it would be best for a fishery to operate is, in fact, essentially an economic and social one, the first stage being to transform the eumetric yield curve into its economic equivalent giving the total value of the annual yield in terms of the total cost of obtaining it. This is itself a major task, and there is as yet little evidence to go on, but it is concluded that to a first approximation both value and cost can be regarded as increasing proportionally with yield and fishing intensity respectively, in which event a eumetric value-cost curve would be similar in shape to the eumetric yield curve from which it is derived. Provided both value and cost are expressed in the same units and plotted on the same scale, the point at which the curve has unit slope is the maximum total profit point. In some fisheries this may be a sufficient objective for regulation, but there may well be other factors to be considered. It may, for example, be better to have a rather larger industry and to absorb some of the potential profit from the fishery by providing employment for more men, obtaining thereby a little greater yield at a lower actual profit. The whole question of defining what are the optimum conditions reduces to one of deciding, for each particular fishery, how much of the maximum potential profit is to be realised as such and how the remainder is to be absorbed.

We turn next (§19.2) to the practical considerations that arise in framing regulative measures designed to bring a fishery to its optimum state. A number of different methods of regulation have been proposed from time to time and although all reduce, in effect, to adjustment either of fishing intensity or gear selectivity, it is shown that some afford a better control and have more predictable results than others (§19.2.1). Perhaps the most important point is that unless it is intended that the industry should continue to operate at the minimum profit level, an essential part of fishery regulation is control of fishing power, even if the direct purpose of a particular measure is to adjust gear selectivity. Otherwise, the greater profitability of fishing caused by the regulation will tend to encourage the building of new ships or the diversion of existing ships from other less profitable fisheries until, again, a state of minimum profit is reached. In the case of a mesh regulation applied to a heavily fished stock, the resulting yield would probably be greater than before but not as high as it would have been had the effort remained constant. The method of catch quotas adopted for the Pacific halibut fishery is taken as an example to illustrate this point. Another problem arising at this stage concerns the immediate effect of a change in fishing intensity or gear selectivity, as opposed to the long-term result that regulation is designed to produce (§19.2.2). Examples are given of these initial phases, based on the transitional yield equations developed in §8.2. There is the need to establish as soon as possible whether the regulative measure has had the effect expected, and to detect any subsequent changes in the fishery that may call for a revision of the regulation. A modification of the statistical control chart technique is offered in §19.2.3 as an objective method of assessing the contemporary state of a fishery in relation to its past behaviour and predictions from theory.

We conclude §19 with a discussion of the regulative problems peculiar to a heterogeneous fishery, that is, one in which a number of independent fleets are operating and perhaps using gear of different kinds and selectivities (§19.3). The North Sea area is, of course, a notable example of this. Methods are developed for assessing the change in yield to each fleet if one alters its fishing intensity or mesh size, and it is shown that attempts at regulation by one fleet usually benefit its non-regulating competitors more than itself—unless it comprises much the greater part of the total fishing effort. This emphasizes the need for all participants in a fishery to make a contribution to its regulation, even though the methods of regulation adopted may not all be the same. If some specific criterion can be agreed between the participants to determine the contribution each shall make, for example, that the yield to each shall increase by the same proportion, it is possible to compute the equivalent changes in fishing intensity and mesh size that would satisfy this criterion.

In §20, the last of our paper, we return to the particular problem of regulation of the North Sea demersal fisheries, and attempt to assess what might be the requirements for optimum fishing. Although the best results would be obtained by fishing each major stock, or group of stocks whose distributions overlap, with the particular eumetric combination of fishing intensity and gear selectivity suited to it, composite regulation of this kind would probably be unworkable at the present time, although it may not be an unreal objective for the future. We therefore consider uniform regulation, whereupon the problem becomes one of determining the best total fishing effort and single size of mesh for all species, assuming that the general pattern of fishing will remain more or less as it is at present.

We derive first the combined eumetric yield curve for plaice and haddock together, and then include cod as representative of the larger species. After making allowance for density dependent effects it is concluded that the combined curve has a well-defined maximum at a fishing intensity about half the pre-war level and with a mesh size in the order of 110 mm. The requirements for the minor species of smaller fish, notably sole and whiting, cannot be assessed in this way, since to obtain the greatest total yield it may be necessary to use a mesh size that would cause an excessive loss of these species. As they support special fisheries such a procedure is impracticable, and it is necessary, by restricting the mesh size, to sacrifice something of the yield of major species, in order at least to maintain the yield of sole and whiting. From provisional assessments for sole it is concluded that a mesh of 80 to 90 mm. in the cod-end of trawls, and appropriate sizes in other gears giving the same selectivity, would not cause any serious loss, and it is reasonable to suppose that the same is true for whiting, although nothing definite can be said at present about this species. This size of mesh would result in a loss of only a few per cent of the maximum combined yield of major species. The conclusion we reach is, therefore, that the greatest total yield of demersal fish from the North Sea, compatible with avoiding any serious loss of sole and whiting, would be obtained by a fishing effort not more than half, and perhaps less, of the pre-war effort and a mesh size of between 80 and 90 mm. Exactly how much greater this yield would be than the present one is more difficult to assess, since as we found earlier the height of the maximum of a yield curve is very much more sensitive to certain density dependent phenomena, notably the relation between recruitment and egg-production, than is the fishing intensity at which it is obtained. A conservative figure would be an increase of some 25% but it might well be as much as 50%. In any event, the benefits would be great because the reduction in fishing effort alone would cause the catch per unit effort to double, even if the yield remained unchanged.

So much, then, for our conception of how much more productive and profitable the North Sea demersal fisheries could be. It is, perhaps, scarcely necessary to emphasize that a prediction such as this, of the effect of a major change in fishing activity, cannot be regarded as an accurate one, although we have tried as far as possible to make allowances for factors that might cause it to be too optimistic. It does, however, establish the scale of regulation that would be required to get the best results from these fisheries; and it is clear that even if it were generally agreed to take something like the changes in fishery effort and gear selectivity mentioned above as the ultimate objective, it would be necessary, for purely practical reasons, to proceed in stages over a period of many years. In the meanwhile, therefore, there is the question of what regulation would constitute a practicable yet real advance in the direction of better utilisation of the North Sea fish resources. Two of the proposals resulting from the 1946 Overfishing Conference seem to fulfil this requirement; one of these is a reduction in overall fishing effort to 85% of the pre-war level, the other an increase in minimum size of mesh to 80 mm. The probable effects of these, separately and together, are shown for plaice, haddock, cod and sole; the greater response to the decrease in fishing intensity would come from plaice and cod, haddock and sole benefiting more from the increased mesh. When the total value of all four species together is considered, the effect of each regulation is about the same—a conservative estimate being an increase of 6%; if, however, both regulations are put into effect, this figure would increase to 10%, equivalent to an extra million or so pounds sterling a year on present day wholesale prices, as a reasonably cautious estimate. The same regulations applied to West coast hake could also be expected to produce a substantial benefit—probably something in excess of an extra half a million pounds sterling a year, shared among the countries concerned. Moreover, the reduction in fishing intensity would allow the catch per unit effort to rise by some 30%, which is enough to be of very real benefit to the fishery industries.

Regulation is bound to produce certain changes in the fish stocks; and these should provide the opportunity of advancing, by research, our understanding of the fisheries to a degree that might be impossible otherwise. Thus, the approach towards optimum fishing and our knowledge of where the optimum lies can be two simultaneous and complementary advances.

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TABLE 9.1

Density of food species and consumption by trout, from Neill (1938). See Figs. 9.1 and 9.2. (p. 131).

	A	B	C	D	E	F	G	H
Species	Nos. per 1,000 sq. cm.				Average Nos. per stomach			
	April	May	June	July	April	May	June	July
Simulium larvae	24	31	211	44	15	3	16	5
Simulium pupae	7	87	73	16	8	30	25	7
Ephemeroptera nymphs	58	34	80	373	16	25	11	7
Trichoptera larvae	6	8	12	20	3	0.5	3	2

TABLE 13.1

Number of plaice of each age-group landed at Lowestoft per 100 hours fishing by British 1st Class steam trawlers, 1929-38. From Thursby-Pelham, 1939. Fish under 23 cm. omitted. (p. 181).

Age-Group / Years (April 1st – March 31st)	II	III	IV	V	VI	VII	VIII	IX	X
1929 – 1930	328	2,120	2,783	1,128	370	768	237	112	48
1930 – 1931	223	2,246	1,938	1,620	302	106	181	58	18
1931 – 1932	95	2,898	3,017	1,150	591	116	100	82	33
1932 – 1933	77	606	4,385	1,186	231	138	42	21	51
1933 – 1934	50	489	1,121	4,738	456	106	80	27	18
1934 – 1935	44	475	1,666	1,538	2,510	160	50	43	14
1935 – 1936	131	1,373	1,595	1,587	1,326	883	144	30	28
1936 – 1937	38	691	2,862	1,094	864	382	436	27	15
1937 – 1938	138	1,293	1,804	1,810	426	390	163	228	26
Average No. in each age-group 1929 – 1938	125	1,355	2,352	1,761	786	339	159	70	28
Nat. log of average No.	4.828	7.212	7.763	7.474	6.667	5.826	5.069	4.249	3.332

TABLE 13.2

Number of haddock of each age-group caught per 10 hours fishing by R.V. EXPLORER, 1923-38. (From Raitt, 1939). (p. 181).

Age-group Years (April 1st – March 31st)	I	II	III	IV	V	VI	VII	VIII
1923 – 1924	49	172	909	131	20	7	5	0.3
1924 – 1925	2,806	39	86	410	82	15	5	1.0
1925 – 1926	1,192	2,386	16	30	149	59	10	3.4
1926 – 1927	964	1,153	851	13	30	64	10	0.4
1927 – 1928	1,550	673	464	353	10	23	31	3.3
1928 – 1929	308	1,543	213	122	55	3	1.8	2.8
1929 – 1930	3,511	249	347	75	33	11	0.1	0.4
1930 – 1931	662	2,760	109	87	21	7	1.6	0.1
1931 – 1932	303	288	455	57	29	6	1.7	0.4
1932 – 1933	1,835	223	159	374	22	9	2.6	1.1
1933 – 1934	318	937	61	55	58	2	1.4	0.3
1934 – 1935	699	167	224	10	11	12	0.2	0.5
1935 – 1936	250	195	45	76	5	4	5	—
1936 – 1937	2,094	73	44	18	32	1	1.1	2.2
1937 – 1938	265	623	29	15	6	11	0.4	0.6
Average No. in each age group 1923 – 1938	1,120	765	267	122	38	16	5.1	1.1
Nat. log of average No.	7.021	6.640	5.587	4.804	3.638	2.773	1.629	0.095

TABLE 13.3

Apparent total mortality coefficients ($F + M$) for plaice, derived from Table 13.1. (p. 181).

Age-Group / Years (April 1st – March 31st)	II/III	III/IV	IV/V	V/VI	VI/VII	VII/VIII	VIII/IX	IX/X	Mean V/VI to IX/X
1929 – 1931	– 1.92	0.09	0.54	1.32	1.25	1.45	1.41	1.83	1.45
1930 – 1932	– 2.56	– 0.30	0.52	1.01	0.96	0.06	0.79	0.56	0.68
1931 – 1933	– 1.85	– 0.41	0.93	1.61	1.45	1.02	1.56	0.47	1.22
1932 – 1934	– 1.85	– 0.62	– 0.08	0.96	0.78	0.55	0.44	0.15	0.58
1933 – 1935	– 2.25	– 1.23	– 0.32	0.64	1.05	0.75	0.62	0.66	0.74
1934 – 1936	– 3.44	– 1.21	0.05	0.15	1.04	0.11	0.51	0.43	0.45
1935 – 1937	– 1.66	– 0.73	0.38	0.61	1.24	0.71	1.67	0.69	0.98
1936 – 1938	– 3.53	– 0.96	0.46	0.94	0.80	0.85	0.65	0.04	0.66
Mean	– 2.38	– 0.67	0.31	0.91	1.07	0.69	0.96	0.60	0.84
*1937 – 1939	–	–	–	1.24	0.92	0.60	0.94	0.67	0.87

* Independent estimate from unpublished data.

TABLE 13.4

Apparent total mortality coefficients ($F + M$) for haddock, derived from Table 13.2. (p. 181).

								Y	Z
Age-Group / Years (April 1st – March 31st)	I/II	II/III	III/IV	IV/V	V/VI	VI/VII	VII/VIII	Mean II/III to VII/VIII	Weighted mean by Jackson's method. II to VIII
1923 – 1925	0.23	0.69	0.80	0.47	0.29	0.34	1.61	0.70	0.67
1924 – 1926	0.16	0.89	1.05	1.01	0.33	0.41	0.39	0.68	0.87
1925 – 1927	0.03	1.03	0.21	0.00	0.85	1.78	3.22	1.18	1.01
1926 – 1928	0.36	0.91	0.88	0.26	0.27	0.72	1.11	0.69	0.87
1927 – 1929	0.00	1.15	1.34	1.86	1.20	2.55	2.40	1.75	1.36
1928 – 1930	0.21	1.49	1.04	1.31	1.61	3.40	1.50	1.73	1.42
1929 – 1931	0.24	0.83	1.38	1.27	1.55	1.93	0.00	1.16	1.15
1930 – 1932	0.83	1.80	0.65	1.10	1.25	1.42	1.39	1.27	1.69
1931 – 1933	0.31	0.59	0.20	0.95	1.17	0.84	0.44	0.70	0.39
1932 – 1934	0.67	1.30	1.06	1.86	2.40	1.86	2.16	1.77	1.49
1933 – 1935	0.64	1.43	1.81	1.61	1.58	2.30	1.03	1.63	1.46
1934 – 1936	1.28	1.31	1.08	0.69	1.01	0.88	0.00	0.83	1.14
1935 – 1937	1.23	1.49	0.92	0.87	1.61	1.29	0.82	1.17	1.21
1936 – 1938	1.21	0.92	1.08	1.10	1.07	0.92	0.61	0.95	1.00
Mean	0.53	1.13	0.96	1.03	1.16	1.47	1.19	1.16	1.12

TABLE 14.1

Values of the function $[2F/\tau(F+X)]\sinh(F+X)\tau/2$ for certain values of F, X and τ. (p. 188).

F	X	τ (yrs.)		
		0.1	0.5	1.0
0.25	0.5	0.25	0.25	0.26
	2.0	0.25	0.26	0.31
	5.0	0.25	0.33	0.65
0.75	0.5	0.75	0.76	0.80
	2.0	0.75	0.81	1.01
	5.0	0.76	1.04	2.30
1.50	0.5	1.50	1.56	1.76
	2.0	1.51	1.70	2.39
	5.0	1.53	2.25	5.94

TABLE 14.2

Liberations and recaptures (n) of marked plaice in rectangles G3, 4 and 5, and H3, 4 and 5, summed in 74-day periods, together with the effective overall fishing intensity ($\bar{f}'$) in the units S.T. ton-hrs./sq. mile/year × 10^{-3}. (p. 216).

No. of marked fish liberated = 11,575		
74 day period	n	$\bar{f}'$
1	1,410	6.003
2	246	5.492

TABLE 14.3

The computation of *c* and *X* by iteration, using (14.19) and (14.20), and data of Table 14.2. (Example). (p. 216).

First stage

A_1	B_1	C_1	D_1	E_1'	F_1	G_1	H_1	J_1	K_1	L_1	$M_1 = c$	$N_1 = X$
n_1	n_2	f'_1	f'_2	N_0	τ	$\frac{B_1 \times C_1}{A_1 \times D_1}$	$-\log G_1$	$1 - G_1$	$\frac{H_1}{F_1}$	$\frac{A_1 \times K_1}{E_1 \times \mathcal{J}_1}$	$\frac{L_1}{C_1}$	$K_1 - L_1$
1,410	246	6.003	5.492	11,575	0.2	0.191	1.656	0.809	8.280	1.247	0.208	7.033

Second and subsequent stages

A_2	B_2	C_2	D_2	E_2	F_2	G_2	H_2	J_2	K_2	L_2	M_2	N_2	P_2	$Q_2 = c$	$R_2 = X$
K_1	$D_1 \times M_1$	$B_2 \times N_1$	$\frac{C_2}{A_2}$	$A_2 \times F_1$	$1 - e^{-E_2}$	$C_2 \times F_1$	$1 - e^{-G_2}$	$\frac{F_2}{H_2}$	$G_1 \times D_2 \times \mathcal{J}_2$	$1 - K_2$	$-\log K_2$	$\frac{M_2}{F_1}$	$\frac{A_1 \times N_2}{E_1 \times L_2}$	$\frac{P_2}{C_1}$	$N_2 - P_2$
8.280	1,142	8.175	0.987	1.656	0.809	1.635	0.805	1.005	0.189	0.811	1.666	8.330	1.251	0.208	7.079
8.280	1.142	8.175	0.987	1.656	0.809	1.635	0.805	1.005	0.189	0.811	1.666	8.330	1.251	0.208	7.079

TABLE 14.4

Liberations and recaptures (n) of marked plaice in rectangle G4, summed in 74-day periods, together with the effective constant fishing intensity (f') in the units S.T. ton-hrs./sq. mile/year × 10^{-3}. (p. 216).

No. of marked fish liberated = 6,717		
74 day period	n	f'
1	950	9.946
2	103	10.879

TABLE 14.5

Liberations and recaptures (n) of marked plaice in rectangle G4, summed in 37-day periods, together with the effective constant fishing intensity (f'). (p. 217).

No. of marked fish liberated = 6,717		
37 day period	n	f'
1	708	7.565
2	242	12.022
3	71	12.706

TABLE 14.6

The double marking experiment: recaptures of two-mark (${}_2n_1$, ${}_2n_2$) and one-mark (${}_1n_{1+2}$) fish, summed in periods of three months, six months and a year. (p. 217).

Recapture period (yrs.) $= \tau$	A	B	C
	${}_2n_1$	${}_2n_2$	${}_1n_1 + {}_2$
1.0	174	19	20
0.5	157	17	12
0.25	134	23	8

TABLE 14.7

Estimates of F, X' and the rate of detachment of marks, L; from data of Table 14.6. (p. 217).

Recapture period (yrs.) $=\tau$	F	X'		L	
		Hyp. (1a)	Hyp. (3a)	Hyp. (1a)	Hyp. (3a)
1.0	0.84	1.16	1.13	0.11	0.24
0.5	1.52	2.63	2.61	0.15	0.32
0.25	2.21	4.44	4.44	0.20	0.40

TABLE 14.8

Estimation of transport coefficients: liberations of fish in rectangle G4 and recaptures in area A (${}_{A}n$) and annulus B (${}_{B}n$), together with the corresponding effective constant and overall fishing intensities ${}_{A}f'$ and ${}_{B}\tilde{f}'$. (p. 219).

Total No. liberated (G4) $= {}_{A}N_0 = 6{,}717$			
${}_{A}n_1$	950	${}_{A}f'_1$	9.946
${}_{A}n_2$	103	${}_{A}f'_2$	10.879
${}_{B}n_1$	165	${}_{B}\tilde{f}'_1$	3.114
${}_{B}n_2$	42	${}_{B}\tilde{f}'_2$	2.651

TABLE 14.9

Commercial statistics of catch and fishing intensity relating to area A and annulus B. (p. 220).

Rectangle	Fishing intensity (hrs. fishing per rect. per year)	Catch of plaice (cwt. per rect. per year)	Density (cwt. plaice per 100 hrs. per rect. per year)
G4 (= area A)	34,783	20,297	58.4
G3, G5, H3, H4, H5 (= annulus B)	9,401	5,634	59.9

TABLE 14.10

Mesh selection of plaice. Ratios of catches of large to small meshed cod-ends. (p. 222).

	A	B	C	D	E	F	G	H
Length (cm.)	Ratios of catch in numbers per hour of large and small meshed cod-ends				Adjusted ogives (see text)			
	72.2 mm. / 43.2 mm.	111.9 mm. / 44.1 mm.	113.0 mm. / 43.2 mm.	140.6 mm. / 44.5 mm.	72.2 mm.	111.9 mm.	113.0 mm.	140.6 mm.
10.5								
11.5								
12.5								
13.5	0.16		0.01		0.11		0.01	
14.5	0.19		0.01		0.13		0.01	
15.5	0.65		0.02		0.45		0.01	
16.5	1.11		0.05		0.78		0.03	
17.5	1.31	0.05	0.04		0.93	0.05	0.03	
18.5	1.52	0.03	0.06		1.09	0.03	0.05	
19.5	1.29	0.06	0.05	0.01	0.94	0.06	0.04	0.01
20.5	1.44	0.05	0.10	0.03	1.05	0.05	0.08	0.02
21.5	1.35	0.06	0.09	0.03	1.00	0.06	0.07	0.03
22.5	1.23	0.11	0.19	0.04	0.92	0.11	0.14	0.03
23.5	1.28	0.16	0.19	0.06	0.97	0.16	0.14	0.05
24.5	1.35	0.37	0.34	0.05	1.03	0.37	0.26	0.04
25.5	1.37	0.69	0.57	0.11	1.06	0.69	0.44	0.09
26.5	1.30	0.79	0.78	0.12	1.02	0.79	0.61	0.10
27.5	0.95	0.93	0.89	0.15	0.75	0.93	0.70	0.12
28.5	2.05	1.08	1.43	0.32	1.64	1.08	1.14	0.26
29.5	1.39	0.95	1.61	0.42	1.12	0.95	1.30	0.35
30.5	1.36	1.27	1.00	0.96	1.11	1.27	0.82	0.80
31.5	1.33	1.08	1.67	0.78	1.10	1.08	1.38	0.65
32.5	1.47	0.72	1.12	0.86	1.23	0.72	0.94	0.72
33.5	1.09	0.90	2.00	0.82	0.92	0.90	1.69	0.68
34.5	1.31	0.58	1.00	1.13	1.12	0.58	0.86	0.94
35.5	0.85	1.20	1.00	1.09	0.73	1.20	0.87	0.91
36.5	0.67	0.50	0.58	1.13	0.59	0.50	0.51	0.94
37.5	1.18	0.33	1.27	1.20	1.05	0.33	1.13	1.00
38.5	1.10	1.33	0.80	0.85	0.99	1.33	0.72	0.71
39.5	1.17	0.67	0.83	1.17	1.06	0.67	0.76	0.97
40.5	1.75	1.50	2.00	2.00	1.62	1.50	1.85	1.67
41.5	1.00	0.50	1.00	0.50	0.94	0.50	0.94	0.42
42.5	0.71		1.00	2.33	0.68		0.95	1.94
43.5	1.20		1.20	1.13	1.15		1.15	0.94
44.5	0.50		2.00	0.50	0.49		1.95	0.42
45.5	1.00		2.00	0.80	0.99		1.97	0.67
46.5				4.00				3.33
47.5				1.00				0.83
48.5		1.00		1.50		1.00		1.25

TABLE 14.11

50% selection lengths and spreads (σ) of the ogives of four experimental cod-end meshes. (p. 224).

A	B	C
Mesh size (mm.)	50% selection length (cm.)	σ (cm.)
72.2	15.6	1.0
111.9	25.0	1.6
113.0	26.0	2.7
140.6	30.5	3.1

TABLE 14.12

Mesh selection of haddock. Catch per 100 hrs. fishing of normal and abnormal meshed cod-ends, and ratios of adjusted catches (col. D). Data of cols. A and B from Davis (1934). (p. 226).

	A	B	C	D
Length (cm.)	Catch per 100 hours fishing		Corrected abnormal catch $\frac{B}{1.272}$	$\frac{C}{A}$
	Normal mesh (70.5 mm.)	Abnormal mesh (83.0 mm.)		
19.5	3.301	0.816	0.642	0.194
20.5	11.84	1.837	1.444	0.122
21.5	35.53	7.142	5.615	0.158
22.5	180.0	45.71	35.94	0.200
23.5	428.7	105.9	83.25	0.194
24.5	731.1	221.4	174.1	0.238
25.5	948.2	426.9	335.6	0.354
26.5	1,387	785.4	617.5	0.445
27.5	1,994	1,454	1,143	0.573
28.5	2,552	2,045	1,608	0.630
29.5	2,904	2,639	2,075	0.715
30.5	2,560	2,613	2,054	0.802
31.5	2,212	2,396	1,884	0.852
32.5	1,591	1,822	1,432	0.900
33.5	1,030	1,368	1,075	1.044
34.5	778.7	1,000	786.2	1.010
35.5	521.8	693.4	545.1	1.045
36.5	444.3	546.1	429.3	0.966
37.5	363.7	417.7	328.4	0.903
38.5	233.0	284.3	223.5	0.959
39.5	183.7	269.4	211.8	1.153
40.5	120.6	145.9	114.7	0.951
41.5	91.26	112.6	88.52	0.970
42.5	66.41	68.97	54.22	0.816
43.5	50.29	52.65	41.39	0.823

TABLE 14.13

Measurements of length and maximum girth of plaice and haddock. (p. 230).

A	B	C	D	E	F	G
Plaice				Haddock		
Girth group (cm.)	No. of fish	Mean length (cm.)	σ of length (cm.)	Girth group (cm.)	No. of fish	Mean length (cm.)
15 – 16	2	18.3	1.91	9 – 10	9	19.6
16 – 17	3	19.8	0.61	10 – 11	83	21.4
17 – 18	4	20.7	1.19	11 – 12	100	22.6
18 – 19	3	23.0	1.23	12 – 13	41	23.5
19 – 20	17	23.1	1.00	13 – 14	8	26.1
20 – 21	15	24.7	0.84	14 – 15	5	29.0
21 – 22	17	25.0	1.13	15 – 16	1	29.0
22 – 23	4	26.4	0.91			
23 – 24	3	26.7	0.62			
24 – 25	3	27.7	0.26			

TABLE 14.14

Standard deviation of mesh size within each of the experimental cod-ends used for plaice. (p. 231).

Mean mesh size (mm.)	σ of mesh size (mm.)
43.2	3.0
44.1	2.6
44.5	3.2
72.2	2.8
111.9	3.5
113.0	3.4
140.6	3.7
Mean	3.2

TABLE 14.15

Total mortality coefficients and fishing effort indices for plaice and haddock. (p. 239). Columns B and D from Tables 13.3 and 13.4, columns C and E from Tables II and IV of Appendix III. The fishing effort indices are in millions of S.T. hours fishing (p. 506, 508).

A	B	C	D	E
	Plaice		Haddock	
Year	Total mortality coefficient	Fishing effort index	Total mortality coefficient	Fishing effort index
1924	—	—	0.68	3.12
1925	—	—	1.18	3.01
1926	—	—	0.69	2.70
1927	—	—	1.75	3.22
1928	—	—	1.73	2.95
1929	1.45	5.81	1.16	2.95
1930	0.68	5.84	1.27	2.99
1931	1.22	4.97	0.70	2.68
1932	0.58	4.91	1.77	2.49
1933	0.74	5.19	1.63	2.90
1934	0.45	4.94	0.83	3.05
1935	0.98	4.63	1.17	3.07
1936	0.66	4.44	0.95	2.86
1937	0.87	4.39	—	2.52
1938	—	4.30	—	—

TABLE 14.16

Total mortality coefficients and fishing effort (gillnet units) for the Fraser River salmon. Columns B from data given by Rounsefell (1949, Table 5), columns C from Rounsefell and Kelez (1938), Table 31). (p. 240).

A	B	C	A	B	C
Year	Total mortality coefficient	Units of gillnet effort	Year	Total mortality coefficient	Units of gillnet effort
1894	0.81	2,481	1915	1.83	4,663
1895	0.90	2,580	1916	2.49	4,299
1896	1.52	4,291	1917	2.83	4,849
1897	1.41	3,832	1918	1.94	3,049
1898	2.03	4,642	1919	1.59	2,600
1899	2.19	4,785	1920	1.34	2,545
1900	2.54	6,369	1921	1.75	2,702
1901	2.48	6,350	1922	1.22	2,548
1902	1.93	4,278	1923	1.08	1,768
1903	2.08	5,362	1924	1.17	1,768
1904	1.94	3,571	1925	1.37	1,689
1905	1.94	4,582	1926	0.74	1,810
1906	1.45	3,178	1927	1.17	2,010
1907	1.63	2,942	1928	1.39	2,092
1908	1.62	2,410	1929	1.47	2,312
1909	2.62	4,634	1930	1.77	2,375
1910	1.58	2,745	1931	1.35	2,163
1911	1.46	2,350	1932	1.21	2,289
1912	1.41	2,476	1933	1.83	2,598
1913	1.68	4,369	1934	1.82	2,745
1914	2.23	4,621			

TABLE 14.17

Total mortality coefficients and fishing effort for the Lake Trout of Opeongo Lake, from Fry (1949, Tables 1 and 5). The fishing effort is in units of 100 boat-hours. (p. 240).

A	B	C
Year	Total mortality coefficient	Fishing effort
1937	1.51	22.4
1938	0.62	16.3
1939	1.41	13.8
1940	1.64	11.7
1941	0.59	11.3
1942	0.46	5.7
1943	0.51	7.1
1944	0.78	9.2
1945	1.55	14.0
1946	0.69	17.4
1947	—	12.3

TABLE 14.18

Successive estimates of M and c (columns B and C) from Table 14.17, and the corresponding sums of squares of residuals U (column D). (p. 240).

A	B	C	D
Estimate	M	c	U
1st	0.377	0.0465	1.628
2nd	0.270	0.0563	1.474
3rd	0.248	0.0583	1.441

TABLE 14.19

Estimation of plaice mortality during 1939-45 war. The mortality figures in columns D to H are exponential coefficients. (p. 242). The Roman numerals in columns A and B indicate the age of the fish.

Port	Sampling month and year	A	B	C	D	E	F	G	H
		Numbers of plaice landed per 100 hrs. fishing by British 1st class steam trawlers		Actual number of fish in post-war samples	Total Mortality	Estimated mortality between pre-war sampling date and Jan. 1940	Estimated mortality between Dec. 1945 and post-war sampling date	Mortality during war D − E − F	Average annual war-time mortality G/6
		Pre-war samples	Post-war samples						
Grimsby	June 1938 and 1946	1,029 (V)	160 (XIII)	8	1.86	1.02	0.50	0.34	0.06
		312 (VI)	120 (XIV)	6	0.96	1.02	0.50	−0.56	−0.09
		50 (VII)	20 (XV)	1	0.92	1.02	0.50	−0.60	−0.10
Lowestoft	July 1938 and 1946	2 328 (V)	207 (XIII)	6	2.42	1.19	0.75	0.48	0.08
		868 (VI)	34 (XIV)	1	3.23	1.19	0.75	1.29	0.22
Lowestoft	October 1938 and 1946	1,574 (V)	159 (XIII)	8	2.29	0.80	1.12	0.37	0.06
		561 (VI)	20 (XIV)	1	3.33	0.80	1.12	1.41	0.24
Grimsby	December 1938 and 1945	663 (VI)	102 (XIII)	1	1.87	0.68	0	1.19	0.20
Lowestoft	December 1938 and 1945	597 (V)	127 (XII)	4	1.55	0.76	0	0.79	0.13
		201 (VI)	63 (XIII)	2	1.13	0.76	0	0.37	0.06
Grimsby	March 1939 and 1946	655 (V)	119 (XII)	4	1.71	0.62	0.32	0.77	0.13
		329 (VI)	119 (XIII)	4	1.02	0.62	0.32	0.08	0.01
		104 (VII)	59 (XIV)	2	0.57	0.62	0.32	−0.37	−0.06
Lowestoft	April 1939 and 1946	1,665 (V)	110 (XII)	3	2.72	0.90	0.26	1.56	0.26
		639 (VI)	147 (XIII)	4	1.47	0.90	0.26	0.31	0.05

TABLE 15.1

Distribution of plaice along the Leman-Haaks Line of stations. (p. 245).

Mean distance from coast (miles)	Mean densities (catch per hour)					Density ratios			
	A	B	C	D	E	F	G	H	J
	Age-Group					Age-Groups			
	I	II	III	IV	V+	I/V+	II/V+	III/V+	IV/V+
18	9.25	59.6	75.9	34.9	20.9	0.443	2.850	3.630	1.670
28	3.03	31.2	50.3	31.6	15.7	0.193	1.990	3.200	2.010
38	1.08	30.8	94.0	62.5	32.0	0.034	0.963	2.940	1.950
49	0.15	21.2	46.3	46.4	32.1	0.005	0.660	1.440	1.450
60	0.00	3.0	13.8	18.1	15.9	0.000	0.187	0.868	1.140
71	0.06	0.8	5.6	9.4	12.7	0.005	0.064	0.440	0.737
82	0.15	1.0	5.1	11.1	8.5	0.020	0.122	0.597	1.300

TABLE 15.2

Leman-Haaks line; linear regression coefficients for logarithms of plaice density ratios on the square of distance from the coast. (p. 249).

Age (t yrs.)	ϑ^{a_0}	ϑ^{a_1}
1.2	– 0.0626	– 0.002210
2.2	– 1.1002	– 0.000632
3.2	– 1.4254	– 0.000368
4.2	– 0.6762	– 0.000111

TABLE 15.3

Estimated numbers of plaice landed each month at Lowestoft and Grimsby per 100 hrs. fishing by 1st class steam trawlers (average for years 1946-48). (p. 258).

	A	B	C	D	E	F	G	H	J	K	L
Age-Group / Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI +
January	0	205	711	1,324	1,158	1,599	1,601	1,048	513	332	609
February	2	885	2,377	2,037	1,581	1,546	1,305	786	555	334	325
March	6	637	1,970	2,240	1,461	1,542	1,265	705	386	286	315
Age-Group / Month	II	III	IV	V	VI	VII	VIII	IX	X	XI +	
April	8	604	2,466	2,544	2,241	1,892	1,197	686	413	447	–
May	4	372	1,543	1,884	1,633	1,509	1,074	667	413	548	–
June	9	1,437	1,800	1,791	1,510	1,171	834	614	376	630	–
July	26	1,138	2,859	1,917	1,275	1,384	1,088	542	335	509	–
August	144	2,221	3,468	1,743	698	626	428	296	231	314	–
September	408	2,413	2,396	1,159	545	395	271	271	139	249	–
October	1,200	1,834	1,715	657	515	563	424	333	167	357	–
November	1,165	1,436	1,197	697	384	358	289	215	187	303	–
December	351	868	880	446	323	367	374	400	167	308	–

TABLE 15.4

Derivation of plaice recruitment curves from data of Table 15.3. (p. 259).

	M	N	O	P	Q	R	S	T	U
Month	Σ Cols. E → L	Σ Cols. F → L	Σ Cols. G → L	$\frac{A}{M}$	$\frac{B}{N}$	$\frac{C}{O}$	Cols. P	Q	R
							smoothed by moving averages of 3		
January	6,860	5,702	4,103	0.0000	0.036	0.173	0.0000	0.138	0.476
February	6,432	4,851	3,305	0.0003	0.182	0.719	0.0004	0.073	0.519
March	5,960	4,499	2,957	0.0010	0.142	0.666	0.0008	0.151	0.761
April	6,876	4,635	2,743	0.0012	0.130	0.899	0.0010	0.120	0.712
May	5,844	4,211	2,702	0.0007	0.088	0.571	0.0012	0.205	0.734
June	5,135	3,625	2,454	0.0018	0.396	0.733	0.0025	0.260	0.820
July	5,133	3,858	2,474	0.0051	0.295	1.156	0.0208	0.621	1.541
August	2,593	1,895	1,269	0.0555	1.172	2.733	0.0929	1.096	2.155
September	1,870	1,325	930	0.2182	1.821	2.576	0.2608	1.329	2.216
October	2,359	1,844	1,281	0.5087	0.995	1.339	0.4660	1.293	1.706
November	1,736	1,352	994	0.6711	1.062	1.204	0.4588	0.865	1.083
December	1,939	1,616	1,249	0.1965	0.537	0.705	0.3012	0.591	0.813

TABLE 15.5

Derivation of seasonal recruitment ogives of plaice from data of Table 15.4 and Fig. 15.9. (p. 260).

	A	B	C	D	E	F	G	H	J
	Relative Abundance of Age-Groups (from Table 15.4 and Fig. 15.9)			A – 0.0	B – 0.5	C – 1.4	$\frac{D}{0.50}$	$\frac{E}{0.90}$	$\frac{F}{0.85}$
Age-Group / Date	I	II	III	I	II	III	I	II	III
January	–	0.50	1.40	–	–	–	–	–	–
February	0.0004	0.50	1.40	0.0004	–	–	0.0008	–	–
March	0.0008	0.50	1.40	0.0008	–	–	0.0016	–	–
Age-Group / Date	II	III	IV	II	III	IV	II	III	IV
April	0.0010	0.50	1.40	0.0010	–	–	0.0020	–	–
May	0.0012	0.50	1.40	0.0012	–	–	0.0024	–	–
June	0.0025	0.52	1.41	0.0025	0.02	0.01	0.0050	0.022	0.012
July	0.0208	0.621	1.541	0.0208	0.121	0.141	0.0416	0.134	0.166
August	0.0929	1.096	2.155	0.0929	0.596	0.755	0.1858	0.662	0.888
September	0.2608	1.329	2.24	0.2608	0.829	0.84	0.5216	0.921	0.988
October	0.4660	1.39	2.25	0.4660	0.89	0.85	0.9320	0.989	1.00
November	0.50	1.40	2.25	0.50	0.90	0.85	1.00	1.00	1.00
December	0.50	1.40	2.25	0.50	0.90	0.85	1.00	1.00	1.00

TABLE 15.6

Derivation of age and length recruitment ogives of plaice from pre-war data (see text for explanation of negative quantities marked *). (p. 261).

	Age-group	II	III	IV	V	VI	VII	VIII	IX	X
A	Catch per 100 hrs. fishing, excluding fish below 23 cm. (from Table 13.1).	125	1,355	2,352	1,761	786	339	159	70	28
B	Percentage of fish below 23 cm. in each age-group in samples, 1929-32.	55.67	25.50	14.10	3.91	0	0	0	0	0
C	Estimated age-composition including small fish.	282	1,816	2,728	1,831	786	339	159	70	28
D	Numbers of recruits into each age-group (catch per 100 hrs. fishing).	639	3,068	2,709	376	*– 145	38	11	* – 2	* – 4
E	Estimated age-composition of recruits = D/ΣD.	0.095	0.459	0.405	0.056	*– 0.022	0.006	0.002	0.000	*– 0.001
F	Age-recruitment ogive = cumulative sum of E.	0.095	0.554	0.959	1.015	0.993	0.999	1.001	1.001	1.000
G	Length in cm. at age of recruitment (see text).	20.6	24.5	28.4	32.1	–	–	–	–	–

TABLE 15.7

Derivation of resultant recruitment ogives of plaice for 70 and 133.5 mm. cod-end meshes. (p. 262).

	A	B	C	D	E	F	G	H
			70 mm. cod-end mesh			133.5 mm. cod-end mesh		
	Length of fish (cm.)	Length recruitment ogive (from row G Table 15.6)	Selection ogive of mesh. (50% selection point = 15.3 cm.)	Product B × C = resultant ogive	1st differences of Column D	Selection ogive of mesh. (50% selection point = 29.1 cm.)	Product B × F = resultant ogive	1st differences of Column G
	14	0.000	0.310	0.000	0.000			
	15	0.000	0.445	0.000	0.000			
	16	0.002	0.610	0.001	0.001			
	17	0.007	0.735	0.005	0.004			
	18	0.020	0.830	0.017	0.012			
	19	0.045	0.890	0.040	0.023			
	20	0.085	0.935	0.079	0.039			
	21	0.160	0.970	0.155	0.076			
	22	0.265	0.995	0.264	0.109	0.000	0.000	0.000
	23	0.375	1.000	0.375	0.111	0.020	0.008	0.008
	24	0.485		0.485	0.110	0.050	0.024	0.016
	25	0.615		0.615	0.130	0.085	0.052	0.028
	26	0.750		0.750	0.135	0.140	0.105	0.053
	27	0.863		0.863	0.113	0.225	0.194	0.089
	28	0.935		0.935	0.072	0.345	0.323	0.129
	29	0.970		0.970	0.035	0.485	0.470	0.147
	30	0.988		0.988	0.018	0.645	0.637	0.167
	31	0.995		0.995	0.007	0.760	0.756	0.119
	32	1.000		1.000	0.005	0.850	0.850	0.094
	33				0.000	0.905	0.905	0.055
	34					0.945	0.945	0.040
	35					0.975	0.975	0.030
	36					0.995	0.995	0.020
	37					1.000	1.000	0.005
	38							0.000
	39							
	40							
J	Mean selection length = L_{ρ}' (cm.) = Σ A × E − 0.5				23.96	Σ A × H − 0.5		29.26
K	Mean selection age = t_{ρ}' (yrs.)				3.72			5.05

TABLE 15.8

Weighting coefficients (u_θ) for plaice and haddock. (p. 267).

A	B	C
θ	u_θ gm.	
	Plaice	Haddock
1	76.60	67.77
2	50.46	34.56
3	30.79	15.12
4	17.71	5.98
5	9.69	2.21
6	5.15	0.79
7	2.62	0.25
8	1.34	0.08
9	0.66	
10	0.34	
11	0.12	
Total	195.48	126.76

TABLE 15.9

Estimates of egg-production and recruitment of haddock (original data from Raitt, 1933, 1939). (p. 269).

A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q	R
Year	Estimated abundance at spawning time (on Apr. 1st, i.e., at the end of each year of life)—mean catch per 10 hours fishing							Estimated number of eggs (× 10^{-10}) laid at each age							Total annual egg-production (× 10^{-12})	Subsequent annual recruits (× 10^{-7})
	2	3	4	5	6	7	8	2	3	4	5	6	7	8		
1922	1,934	532	112	42	39	2.3	2.9	236	1,429	614	333	389	27	38	30.7	3.9
1923	193	1,297	223	54	17	5.5	0.4	24	3,483	1,221	429	169	64	5	54.0	224.4
1924	44	129	659	106	17	6.0	3.0	5	346	3,607	842	169	69	40	50.8	95.3
1925	2,596	27	58	279	70	12.5	4.2	316	73	317	2,216	698	144	55	38.2	77.1
1926	1,172	1,618	14	30	106	34.5	5.2	142	4,345	77	238	1,057	400	68	63.3	123.9
1927	818	808	602	11	26	47.5	6.6	100	2,170	3,296	87	260	551	87	65.5	24.6
1928	1,546	443	293	204	6	12.4	16.9	188	1,190	1,604	1,620	60	143	224	50.3	280.7
1929	278	945	144	77	33	1.5	1.1	34	2,538	788	611	329	17	14	43.3	52.9
1930	3,135	179	217	48	20	6.3	0.1	381	481	1,188	381	200	73	1	27.1	24.2
1931	475	1,607	83	58	13	4.3	1.0	58	4,315	454	460	129	50	13	54.8	146.7
1932	263	223	414	39	19	4.3	1.4	31	598	2,266	309	189	50	18	34.6	25.4
1933	1,386	142	107	216	12	5.2	1.4	168	381	585	1,716	119	61	18	30.5	55.9
1934	242	580	35	33	35	1.1	0.9	29	1,557	191	262	349	13	12	24.1	20.0
1935	447	106	150	7	7	8.5	0.1	54	285	821	55	69	99	1	13.8	167.4
1936	161	119	31	54	3	2.5	3.6	20	319	169	429	30	29	48	10.4	21.2
1937	1,358	51	29	12	21	0.7	0.8	165	137	159	96	210	8	11	7.9	15.6
														Means	37.5	84.95

TABLE 15.10

Factors for converting haddock age-composition data into estimates of egg-production (see Table 15.9). (p. 271).

A	B	C	D	E	F
Age at spawning (yrs.)	s	p	χ	w	$(B \times C \times D \times E \times 7.16 \times 10^5) \times 10^{-8}$
2	0.5	0.11	267	116	12.2
3	0.5	0.75	485	206	268
4	0.5	0.96	520	306	547
5	0.5	0.99	537	417	794
6	0.5	1.00	521	534	996
7	0.5	1.00	521	621	1,158
8	0.5	1.00	521	708	1,321

TABLE 16.1

Weight-length relationship in plaice; data from Lowestoft market samples in 1946. (p. 281).

A	B	C	D
Length (cm.)	No. in sample	Av. weight (gm.)	Calc. weight (gm.) ($w = 0.00892l^3$)
23.5	20	124	116
24.5	57	146	131
25.5	111	155	148
26.5	172	174	166
27.5	241	190	186
28.5	237	213	206
29.5	294	236	229
30.5	346	259	253
31.5	416	284	279
32.5	476	308	306
33.5	649	332	335
34.5	656	363	366
35.5	567	391	399
36.5	491	419	434
37.5	382	455	470
38.5	290	500	509
39.5	307	538	550
40.5	236	574	593
41.5	183	623	638
42.5	147	674	685
43.5	87	724	734
44.5	88	808	786
45.5	51	812	840
46.5	38	909	897
47.5	41	1,039	956
48.5	27	1,124	1,018
49.5	25	1,163	1,082

TABLE 16.2

Average weight of plaice in each age-group; Lowestoft and Grimsby market samples, 1929-1938. (p. 282).

Calendar Year	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	IX	XX
1929	167	190	218	270	289	392	574	665	802	1,143	1,067	1,116	1,237	1,275	1,230	1,464	1,452	1,438	1,568
1930	136	190	257	340	441	498	582	740	961	1,285	1,153	1,201	1,215	1,246	1,459	1,600	1,550	–	–
1931	127	152	221	349	440	503	593	675	809	964	1,139	1,326	1,186	1,643	1,589	1,676	1,557	1,349	1,681
1932	132	143	182	297	421	535	641	721	827	980	1,058	1,325	1,285	1,223	1,556	1,530	1,517	1,777	1,170
1933	146	165	189	251	383	528	645	787	818	1,037	1,045	1,290	1,487	1,574	1,504	1,953	1,692	1,539	–
1934	157	189	202	229	277	521	711	798	819	950	1,038	1,346	1,380	1,411	1,540	1,749	1,381	1,692	1,664
1935	154	178	214	280	313	383	643	789	876	1,104	1,064	1,202	1,430	1,457	1,553	1,789	1,723	1,920	1,942
1936	149	171	198	255	338	377	467	781	885	1,176	1,083	1,042	1,354	1,714	1,541	1,492	1,633	2,028	1,475
1937	160	173	222	310	383	490	519	624	845	1,048	1,179	1,286	1,379	1,453	1,691	1,558	1,835	2,008	2,243
1938	163	187	223	288	390	487	609	751	801	1,220	1,239	1,239	1,443	1,456	1,668	1,597	1,577	2,048	1,450
Mean 1929 – 38	149	172	210	285	368	474	601	736	840	1,077	1,106	1,246	1,348	1,472	1,553	1,653	1,604	1,755	1,681

TABLE 16.3

Fit of von Bertalanffy equation to weight-at-age data for plaice given in Table 16.2. (p. 283).

A	B	C	D	E	F	G	H
Age (yrs.)	Observed weight (gm.)	$w_t^{1/3}$	$14.206 - w_t^{1/3}$	log D	Theoretical weight (gm.)	Estimated length (cm.)	Theoretical length (cm.)
2.7	149	5.301	8.905	2.187	66	25.6	19.4
3.7	172	5.561	8.645	2.157	122	26.8	23.9
4.7	210	5.944	8.262	2.112	194	28.7	27.9
5.7	285	6.581	7.625	2.031	281	31.7	31.6
6.7	368	7.166	7.040	1.952	381	34.6	35.0
7.7	474	7.797	6.409	1.858	489	37.6	38.0
8.7	601	8.439	5.767	1.752	604	40.7	40.8
9.7	736	9.029	5.177	1.644	724	43.5	43.3
10.7	840	9.435	4.771	1.562	844	45.5	45.6
11.7	1,077	10.250	3.956	1.375	964	49.4	47.6
12.7	1,106	10.342	3.865	1.352	1,085	49.9	49.5
13.7	1,246	10.761	3.445	1.237	1,201	51.9	51.3
14.7	1,348	11.047	3.159	1.150	1,314	53.3	52.8
15.7	1,472	11.376	2.831	1.040	1,423	54.8	54.2
16.7	1,553	11.580	2.626	0.9654	1,527	55.8	55.5
17.7	1,653	11.824	2.382	0.8252	1,626	57.0	56.7
18.7	1,604	11.706	2.500	0.9164	1,720	56.4	57.8
19.7	1,755	12.062	2.144	0.7626	1,808	58.2	58.7
20.7	1,681	11.890	2.316	0.8397	1,891	57.3	59.6

TABLE 16.4

Additional weight-at-age data for young plaice, and theoretical values. (p. 284).

Age (yrs.)	Weight (gm.)		
	Wallace	Thursby-Pelham	Theoretical
1.2	8	–	15
2.0	34	–	37
2.2	40	36	44
3.0	81	–	81
3.2	106	69	92

TABLE 16.5

Average length-at-age of haddock, and fit of the von Bertalanffy equation; data of column B for ages 2-6 from Raitt (1933), for 1 year fish* from Raitt (1939). (p. 285).

A	B	C	D	E
Age (yrs.)	Observed length (cm.)	Theoretical length (cm.)	Estimated weight (gm.)	Theoretical weight (gm.)
1.0	17.0*	17.9	39.9	46.6
2.0	24.5	24.3	119.4	116.5
3.0	29.5	29.5	208.5	208.5
4.0	33.5	33.8	305.3	313.5
5.0	37.0	37.2	411.3	418.0
6.0	40.0	40.1	519.7	523.6

TABLE 16.6

Growth data of North Sea cod: modal lengths in column B from Graham (1934). (p. 286).

A	B	C	D
Age (yrs.)	Observed modal length (cm.)	Calculated weight (gm.)	Theoretical weight (gm.)
1.0	18	51	51
2.0	36	465	477
3.0	55	1,446	1,446
4.0	68	2,732	2,855
5.0	78	4,124	4,618
6.0	88	6,125	6,335

TABLE 16.7

Growth data of North Sea sole; observed lengths in column B from Bückmann (1934). (p. 286).

A	B	C	D
Age (yrs.)	Observed length (cm.)	Calculated weight (gm.)	Theoretical weight (gm.)
1	9.5	7.7	8.0
2	19.6	61.7	64.1
3	25.3	144.9	150.4
4	28.3	225.2	236.4
5	32.3	301.9	307.8
6	34.3	361.6	361.8
7	35.5	402.6	400.3
8	36.5	437.6	427.2

TABLE 16.8

Observed average weight of all plaice in age-groups II-V, and estimated average weight of recruits into those age-groups. (p. 289).

A	B	C	D	E	F	G
Age Group	Observed average weight in October (gm.)	Estimated average weight (gm.) of recruits, according to			W_∞ (gm.)	K
		Hypothesis (j)	Hypothesis (k)	Hypothesis (l)	Hypothesis (k)	Hypothesis (l)
II	151	151	151	151	7,921	0.144
III	168	162	156	158	4,450	0.115
IV	202	176	160	165	2,753	0.095
V	270	170	114	130	1,318	0.072

TABLE 16.9

Observed and predicted distributions of weight among plaice of the same age. (p. 291).

A	B	C	D	E	F	G	H	J	K	L	M	N	P
Age (yrs.)	Mean weight $= \bar{w}$ (gm.)					Standard deviation of weight $= \sigma$ (gm.)				Coefficient of variation $= \sigma/\bar{w} \times 100$			
	(j)	(k)	(l)	Observed (Pre-war)	Observed (Post-war)	(j)	(k)	(l)	Observed (Post-war)	(j)	(k)	(l)	Observed (Post-war)
5.7	303	305	304	285	325	61	128	104	114	20	42	34	35
6.7	404	412	408	368	398	68	173	132	153	17	42	32	38
7.7	513	529	520	474	495	72	223	159	179	14	42	31	36
8.7	628	653	638	601	640	75	275	184	284	12	42	29	44
9.7	747	782	759	736	749	77	329	207	345	10	42	27	46
10.7	868	912	881	840	824	78	384	227	329	09	42	26	40

TABLE 16.10

Weight-at-age of certain year-classes of plaice to compare pre-war and war-time growth. Estimates of W_∞ for war period in column F; for pre-war periods of similar duration in columns J, M, P and S. (p. 293).

			Post-War Sampling Year			Pre-War Sampling Years											
			1946			1938			1937			1936			1935		
A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q	R	S
Age (yrs.)	Theoretical weight (gm.)	Age (yrs.)	Year Class	Weight (gm.)	W_∞ (gm.)	Year Class	Weight (gm.)	W_∞ (gm.)	Year Class	Weight (gm.)	W_∞ (gm.)	Year Class	Weight (gm.)	W_∞ (gm.)	Year Class	Weight (gm.)	W_∞ (gm.)
3.7	122	10.7	1936	802	2,672	1928	801	2,668	1927	845	2,871	1926	885	3,059	1925	876	3,016
4.7	194	11.7	1935	858	2,425	1927	1,220	3,997	1926	1,048	3,231	1925	1,176	3,798	1924	1,104	3,477
5.7	281	12.7	1934	729	1,559	1926	1,239	3,497	1925	1,179	3,252	1924	1,083	2,868	1923	1,064	2,793
6.7	381	13.7	1933	970	2,051	1925	1,239	3,009	1924	1,286	3,185	1923	1,042	2,298	1922	1,202	2,872
	Mean				2,177			3,293			3,135			3,006			3,040

TABLE 16.11

Growth and density of haddock, from Raitt (1939). Estimates of L_∞ for each age-group in each year and the corresponding number-density indices (catch per 1/100 hr. fishing). (p. 297).

A	B	C	D	E	F
Area	Sampling Year	L_∞ for age-group (cm.)			Density Index
		I	II	III	
West	1927	61.4	45.5	—	3.137
	1928	61.6	59.0	50.9	1.983
	1929	56.0	60.5	44.8	5.554
	1930	57.1	49.8	47.8	4.114
	1931	61.8	53.9	49.0	0.983
	1932	58.9	52.2	44.4	3.394
	1933	61.7	51.5	60.5	1.956
	1934	69.4	54.9	64.0	0.844
	1935	69.8	57.9	60.3	0.476
	1936	63.6	63.8	59.1	2.643
	1937	63.3	57.5	67.1	1.498
	Mean	62.2	55.1	54.8	2.417
Central	1927	57.1	51.4	—	3.763
	1928	61.8	46.4	48.9	2.823
	1929	47.1	47.7	40.8	6.022
	1930	53.6	45.3	46.0	3.949
	1931	57.9	51.0	49.0	1.897
	1932	57.5	51.5	45.1	2.748
	1933	57.8	53.2	58.6	2.202
	1934	66.6	55.2	50.1	1.272
	1935	67.1	56.9	49.6	0.695
	1936	56.2	58.9	53.7	2.534
	1937	59.3	49.4	50.4	1.175
	Mean	58.4	51.5	49.2	2.644
East	1928	66.9	48.0	25.1	2.053
	1929	46.9	43.9	33.8	2.297
	1930	67.2	58.0	58.5	2.764
	1931	72.9	60.0	65.6	0.762
	1932	64.1	75.0	72.9	2.002
	1933	54.7	41.5	17.5	0.639
	1934	64.8	59.5	58.5	1.192
	Mean	62.5	55.1	47.4	1.673

TABLE 16.12

Maintenance requirements of plaice; from Dawes (1930, 1931). Estimation of [illegible] and [illegible] (p. [illegible]).

x	y	x	y	x	y
Average weight (gm.)	Daily ration (gm.)	Average weight (gm.)	Daily ration (gm.)	Average weight (gm.)	Daily ration (gm.)
17.6	1.4	42.3	0.7	78.6	1.1
19.8	0.43	43.6	0.7	94.4	0.95
21.2	0.4[illegible]	44.0	0.64	98.4	1.27
22.3	0.4	51.4	0.50	102.7	1.0
29.8	0.8	52.2	0.9	106.1	1.3
30.1	0.6	58.5	0.8	107.3	1.3
33.7	0.46	61.8	0.88	113.6	1.41
38.6	0.9	64.8	0.9	113.6	1.4
41.5	0.6	69.5	0.87	129.7	1.4
42.0	0.5	71.8	1.2	134.4	1.24

TABLE 16.13

Efficiency of utilisation of food for growth in the plaice; from Dawes (1931). Estimation of ε. (p. 302).

A	B	C	D	E	F	G
Fish	Weight (gm.)	Weight increment (gm.)	Food eaten during period (gm.)	Length of period (days)	Calculated maintenance food (gm.)	Food for growth D – F (gm.)
D3	15.5	—	—	—	—	—
(1929)	18.0	2.5	22.0	14	5.1	16.9
♂	22.5	4.5	26.0	15	6.3	19.7
	30.0	7.5	36.0	14	6.9	29.1
	37.0	7.0	41.4	14	8.2	33.2
	41.5	4.5	44.2	14	9.1	35.1
Table 67	51.5	10.0	53.2	14	10.2	43.0
(Dawes)	65.5	14.0	68.5	17	14.4	54.1
	79.0	13.5	65.2	15	14.6	50.6
	90.0	11.0	76.5	14	15.1	61.4
	95.5	5.5	63.0	14	16.1	46.9
	103.0	7.5	50.0	15	18.0	32.0
	105.0	2.0	39.0	15	18.6	20.4
B1	24.0	—	—	—	—	—
(1929)	31.0	7.0	40.0	15	7.7	32.3
♀	35.0	4.0	22.0	14	8.1	13.9
	40.0	5.0	26.0	15	9.4	16.6
	47.0	7.0	38.0	14	9.7	28.3
	53.5	6.5	44.3	14	10.7	33.6
Table 68	61.0	7.5	46.2	14	11.7	34.5
(Dawes)	69.0	8.0	57.0	14	12.7	44.3
	79.5	10.5	69.0	17	16.9	52.1
	89.5	10.0	66.9	15	16.2	50.7
	96.0	6.5	63.0	14	16.1	46.9
	98.5	2.5	49.0	14	16.6	32.4
	104.0	5.5	54.0	15	18.3	35.7
	105.5	1.5	43.0	14	17.5	25.5
B4	18.5	—	—	—	—	—
(1929)	26.0	7.5	40.0	15	6.7	33.3
♀	32.0	6.0	22.0	14	7.4	14.6
	36.5	4.5	26.0	15	8.9	17.1
	43.0	6.5	36.5	14	9.2	27.3
	50.5	7.5	48.7	14	10.2	38.5
Table 69	60.5	10.0	51.4	14	11.4	40.0
(Dawes)	66.0	5.5	54.3	14	12.5	41.8
	76.0	10.0	65.5	17	16.4	49.1
	83.5	7.5	55.2	15	15.6	39.6
	90.0	6.5	59.0	14	15.4	43.6
	102.0	12.0	63.0	14	16.5	46.5
	108.0	6.0	52.5	15	18.7	33.8

TABLE 16.14

Fit of Kostitzin's equation to data of growth and food consumption in plaice. Estimation of $1/k$ and ε_0 (all fish). (p. 303).

A	B	C	D	E	F	G	H	J	K
Fish	Mid Wt. (gm.) $= \bar{w}$	Δw (gm.)	$\frac{\Delta w}{\Delta t}$	$\Delta \xi$ (gm.)	$\frac{\Delta \xi}{\Delta t}$	$\zeta \bar{w}^{2/3}$ (gm.)	$k\varepsilon_0$	$\frac{1}{k}$	ε_0
D3	25	10.0	183	50	913	175	0.00208	305	0.63
B4		9.5	173	40	730				
I3		2.75	50.2	15	274				
D3	30	11.25	205	54	986	198	0.00200	320	0.64
B1		8.25	151	44	803				
B4		8.0	146	31	566				
I3		6.0	110	25	456				
D3	35	9.0	164	59	1,077	219	0.00292	346	1.01
B1		6.0	110	33	602				
B4		6.25	114	38	694				
I3		6.75	123	32	584				
I4		6.75	123	23	420				
D3	40	8.25	151	68	1,241	239	0.00212	296	0.63
B1		7.75	141	45	821				
B4		9.0	164	56	1,022				
I1		5.0	91.3	23	420				
I2		2.5	45.6	22	402				
I3		6.75	123	32	584				
I4		5.0	91.3	30	548				
D3	45	13.25	242	75	1,369	259	0.00127	336	0.43
B1		9.25	169	57	1,040				
B4		11.0	201	65	1,186				
I1		6.0	110	32	584				
I2		3.75	68.4	32	584				
I3		5.5	100	33	602				
I4		7.75	141	33	602				
D3	50	15.5	283	77	1,405	278	0.00110	353	0.39
B1		10.0	183	62	1,132				
B4		13.0	237	70	1,278				
I1		5.25	95.8	32	584				
I2		2.5	45.6	34	621				
I3		5.5	100	36	657				
I4		6.75	123	33	602				
D3	55	16.5	301	77	1,405	296	0.00093	413	0.38
B1		10.5	192	64	1,168				
B4		13.25	242	73	1,332				
I1		3.5	63.9	33	602				
I3		6.75	123	35	639				
I4		6.0	110	33	602				
D3	60	16.5	301	79	1,442	314	0.00132	440	0.58
B1		11.75	214	72	1,314				
B4		11.25	205	74	1,351				
I1		7.5	137	37	675				
I4		8.0	146	36	657				

TABLE 16.15

Fit of Kostitzin's equation to data of growth and food consumption in plaice. Estimation of $1/k$, ε_0, ε_m and $W_{\infty M}^{1/3}$ (fish I_2 excluded). (p. 304).

A	B	C	D	E	F	G
Fish	Mid wt. (gm.) $= \bar{w}$	$k\varepsilon_0$	$1/k$ (gm.)	ε_0	ε_m	$W_{\infty M}^{1/3}$ (gm.)
D3 B1 B4 I1 I3 I4	40	0.00239	329	0.785	0.710	50.1
	45	0.00139	349	0.485	0.465	66.9
	50	0.00100	395	0.395	0.385	78.2
	55	0.00097	407	0.395	0.384	75.0
			Means	0.515	0.486	67.6

TABLE 16.16

Estimation of the limiting growth coefficient, $W_{\infty L}^{1/3}$, from data of Table 16.13. (p. 306).

A	B	C	D	E	F
Fish	w_1 (gm.)	w_2 (gm.)	t (yrs.)	$W_{\infty L}^{1/3}$ (gm.)	$W_{\infty L}^{1/3}$ (gm.)
D3	15.5	105.0	0.479	52	27
B1	24.0	105.5	0.518	41	23
B4	18.5	108.0	0.479	50	26

TABLE 18.1

Plaice. Stages in the computation of yield from (8.7) and (8.8), using the short-step approximation to the selection ogive, with $F_\infty = 0.73$ and $t_{\rho'} = 3.72$ years. (p. 331).

A	B	C	D	E	F	G	H
Length (cm.)	Age (yrs.)	Resultant recruitment ogive (Table 15.7 col. D)	Δt	F_y/F_∞	Values of F_y	Values of $(Y_W)_y/N_y$ (gm.)	Values of N_y/R
15	1.787	0					
			0.199	0.0005	0.0004	0.002	1.000
16	1.986	0.001					
			0.202	0.003	0.002	0.02	0.980
17	2.188	0.005					
			0.206	0.011	0.008	0.09	0.960
18	2.394	0.017					
			0.211	0.028	0.021	0.25	0.939
19	2.605	0.040					
			0.215	0.059	0.043	0.53	0.915
20	2.820	0.079					
			0.219	0.117	0.085	1.35	0.888
21	3.039	0.155					
			0.224	0.209	0.153	3.33	0.852
22	3.263	0.264					
			0.229	0.319	0.233	4.95	0.806
23	3.492	0.375					
			0.234	0.430	0.314	8.23	0.746
24	3.726	0.485					
			0.239	0.550	0.401	12.43	0.677
25	3.965	0.615					
			0.246	0.682	0.498	17.28	0.601
26	4.211	0.750					
			0.250	0.806	0.589	21.77	0.519
27	4.461	0.863					
			0.258	0.899	0.656	29.16	0.437
28	4.719	0.935					
			0.263	0.952	0.695	33.49	0.359
29	4.982	0.970					
			0.269	0.979	0.715	38.93	0.291
30	5.251	0.988					
			0.277	0.991	0.724	45.03	0.234
31	5.528	0.995					
			0.284	0.998	0.728	51.36	0.186
32	5.812	1.000					
			9.188	1.000	0.730	367.7	0.147
68.5	15.000	1.000					

$Y_W/R = \Sigma\,(\text{G} \times \text{H}) = 155.3$ (gm.)

TABLE 18.2

Plaice. Yield per recruit, Y_W/R (gm.), at various values of F_∞, resulting from the use of different methods of approximating to the selection ogive. (For explanation see text p. 332).

A	B	C	D	E	F
	$t_{\rho'} = 3.72$ yrs.			$t_{\rho'} = 10$ yrs.	
F_∞	Knife-edge	Discontinuous	Linear regression	Knife-edge	Linear regression
0	0	0	0	0	0
0.05	118.4	118.0	115.6	78.9	77.5
0.10	177.0	175.9	176.1	140.2	139.2
0.20	211.7	211.6	211.2	224.6	223.3
0.30	207.6	205.4	207.1	275.2	273.2
0.40	194.7	191.5	193.0	305.0	303.4
0.50	182.2	177.4	181.2	323.0	320.2
0.73	160.2	155.3	158.4	340.2	335.7
0.75	159.1	154.6	156.5	340.8	335.8
1.00	145.5	138.9	142.5	344.9	339.5
1.50	131.1	120.8	126.5	343.6	336.7
∞	101.3	30.2	65.9	333.7	298.7

TABLE 18.3

Plaice. Stages in computing by iteration the yield per recruit, Y_W/R, with natural mortality density dependent. Columns E, F and G give solutions for M obtained by the various methods explained in the text. (p. 334).

A	B	C	D	E	F	G
F	${}_1\bar{P}_N/R$ (${}_1M = 0.1$)	${}_2M$	${}_2\bar{P}_N/R$	M	M	$\underline{M}$
0	6.762	0.2000	4.476	0.2000	0.2000	0.2000
0.01	6.463	0.1946	4.401	0.1970	0.1961	0.1957
0.05	5.439	0.1762	4.076	0.1849	0.1818	0.1818
0.10	4.476	0.1589	3.654	0.1712	0.1670	0.1666
0.20	3.220	0.1363	2.907	0.1492	0.1447	0.1447
0.30	2.473	0.1228	2.345	0.1333	0.1296	0.1295
0.40	1.993	0.1142	1.939	0.1216	0.1190	0.1189
0.50	1.665	0.1083	1.642	0.1130	0.1114	0.1113
0.73	1.205	0.1000	1.205	0.1000	0.1000	0.1000
0.75	1.176	0.0995	1.177	0.0991	0.0993	0.0992
1.00	0.909	0.0947	0.914	0.0911	0.0924	0.0922
1.50	0.625	0.0896	0.629	0.0824	0.0849	0.0850

TABLE 18.4

Plaice. Density dependent natural mortality; maximum possible values of M in the virgin stock ($F = 0$) for various values of M in the pre-war population with $F = 0.73$, using a linear relationship between M and population numbers. (p. 335).

M at $F = 0.73$	M at $F = 0$, ($\mu_1 = 0$)	$\mu_2 R$
0.05	0.198	0.039
0.10	0.288	0.083
0.20	0.431	0.186
0.30	0.556	0.309

TABLE 18.5

Plaice. Density dependent natural mortality; solutions for M for various values of $t_{\rho'}$, with F constant at 0.73. (p. 336).

t_ρ' (yrs.)	M
3.72	0.100
4	0.107
5	0.130
6	0.147
8	0.172
10	0.186
12	0.195
14	0.199
15	0.200

TABLE 18.6

Plaice. Yield per recruit, Y_W/R (gm.), taking into account the relative recruitment into age-groups II to V, and for various hypotheses defining the subsequent growth of each recruit sub-group. Columns F and G are reproduced in text. (p. 338).

F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	G
	Hypothesis (j)						Hypothesis (k)						Hypothesis (l)						Y_W/R for $t_{\rho'} = 3.72$ (yrs.) $W_\infty = 2{,}867$ (gm.) $K = 0.095$
	Yield (gm.) from fish recruited into age-group				Total (gm.)	Total reduced to 194.4 at $F = 0.73$	Yield (gm.) from fish recruited into age-group				Total (gm.)	Total reduced to 194.4 at $F = 0.73$	Yield (gm.) from fish recruited into age-group				Total (gm.)	Total reduced to 194.4 at $F = 0.73$	
	II	III	IV	V			II	III	IV	V			II	III	IV	V			
0.01	4.3	19.4	16.0	2.0	41.6	32.9	8.7	25.6	15.0	1.1	50.4	38.7	6.0	22.5	15.6	1.4	45.5	35.1	36.9
0.05	16.2	75.5	63.5	7.8	163.0	128.9	32.4	98.4	59.6	4.3	194.7	149.5	22.9	87.4	62.1	5.6	178.0	137.2	143.8
0.10	23.8	112.8	97.2	12.3	246.1	194.6	46.2	145.2	91.0	6.8	289.2	222.0	33.4	130.1	94.8	8.8	267.1	205.8	214.8
0.20	27.8	136.0	120.9	15.7	300.4	237.5	50.7	169.9	112.9	8.9	342.4	262.9	38.5	155.0	117.6	11.3	322.4	248.4	257.2
0.30	27.1	134.4	122.3	16.2	299.9	237.1	46.2	163.2	113.9	9.3	332.6	255.4	36.8	151.6	118.6	11.7	318.7	245.6	251.9
0.40	25.5	127.7	117.7	15.7	286.6	226.6	41.0	151.1	109.3	9.2	310.6	238.5	33.9	142.2	113.8	11.4	301.3	232.2	236.2
0.50	23.9	120.8	112.0	15.1	271.7	214.8	36.5	139.6	103.7	8.9	288.7	221.7	31.2	133.0	108.0	10.9	283.1	218.1	221.0
0.73	21.4	108.6	102.0	13.7	245.7	194.4	29.8	120.8	94.2	8.4	253.2	194.4	26.8	117.3	98.1	10.1	252.3	194.4	194.4
0.75	21.2	107.9	101.2	13.6	243.9	192.8	29.4	119.6	93.4	8.3	250.7	192.5	26.5	116.3	97.2	10.0	250.0	192.6	193.1
1.00	19.7	100.3	94.4	12.7	227.1	179.5	25.5	108.3	87.0	7.9	228.7	175.6	23.6	106.3	90.6	9.4	229.9	177.1	176.6
1.50	18.0	92.2	87.1	11.7	208.9	165.1	21.6	96.2	79.9	7.4	205.1	157.5	20.6	95.5	83.3	8.7	208.1	160.3	159.1

TABLE 18.7

Plaice and haddock. Density dependent growth; solutions for W_∞ at various values of F, mesh constant at 70 mm. In addition, values of $t_{\rho'}$ are shown for haddock, since this parameter varies with W_∞ even though the mesh size is held constant. (p. 342).

A	B	C	D
	Plaice	Haddock	
F	W_∞ (gm.)	W_∞ (gm.)	$t_{\rho'}$ (yrs.)
0	808	880	2.00
0.01	852		
0.05	1,035	917	1.97
0.10	1,270	951	1.95
0.20	1,720	1,009	1.92
0.30	2,093	1,055	1.90
0.40	2,381	1,092	1.88
0.50	2,578	1,122	1.87
0.73	2,867		
0.75	2,882	1,175	1.85
1.00	3,039	1,209	1.83
1.50	3,170	1,249	1.82
∞	3,395	1,348	1.78

TABLE 18.8

Plaice and haddock. Density dependent growth; solutions for W_∞ and $t_{\rho'}$ for various mesh sizes, with $F = 0.73$ in plaice and 1.0 in haddock. (p. 345).

A	B	C	D	E	F
Plaice			Haddock		
Cod-end mesh (mm.)	W_∞ (gm.)	$t_{\rho'}$ (yrs.)	Cod-end mesh (mm.)	W_∞ (gm.)	$t_{\rho'}$ (yrs.)
80.0	2,867	3.72	53.9	1,328	1.00
105.0	2,765	4.01	70.0	1,209	1.83
132.5	2,359	5.15	85.0	1,095	2.86
149.7	1,854	6.69	100.0	977	4.36
173.1	808	15.00	115.0	881	6.76
			128.4	880	10.00

TABLE 18.9

Plaice. Growth dependent on food consumption and availability; solutions for W_∞ at various values of F; mesh constant at 70 mm. Hypotheses (b), (c), (d), (e), (f_1) and (f_2). (p. 347).

A	B	C	D	E	F	G	H
F	Ξ/R (m-g-e-s.) (W_∞=2,867 gm.)	W_∞ (gm.) hyp. (b)	W_∞ (gm.) hyp. (c)	W_∞ (gm.) hyp. (d)	W_∞ (gm.) hyp. (e)	W_∞ (gm.) hyp. (f_1)	W_∞ (gm.) hyp. (f_2)
0	11,003	808	$< W_p'$	$< W_p'$	1,090	425	123
0.01	10,393	852	,,	,,	1,105	480	140
0.05	8,317	1,035	,,	,,	1,185	690	250
0.10	6,470	1,270	,,	,,	1,285	1,010	440
0.20	4,169	1,720	,,	,,	1,530	1,680	950
0.24			,,	123			
0.27		1,982				1,982	
0.30	2,920	2,093	,,	210	1,785	2,100	1,550
0.34			123				
0.40	2,180	2,381	210	520	2,120	2,360	2,000
0.50	1,713	2,578	650	1,050	2,335	2,570	2,350
0.73	1,122	2,867	2,867	2,867	2,867	2,867	2,867
0.75	1,088	2,882	3,150	3,050	2,910	2,890	2,910
1.00	788	3,039	9.200	5,850	3,380	3,010	3,180
1.50	502	3,170	–	–	(4,200)	3,140	3,440

TABLE 18.10

Plaice. Estimates of Y_W/R (gm.) for certain values of F with mesh constant at 70 mm., obtained from various hypotheses concerning the relationship between growth, food consumption and food availability. See Fig. 18.13 and Table 18.9. (p. 351).

F	Curve (a)	Curve (b)	Curve (e)	Curve (f_1)	Curve (f_2)
0.01	37	18	21	13	8
0.05	144	80	85	64	42
0.1	215	136	137	121	84
0.2	257	197	187	195	151
0.3	252	217	203	218	191
0.4	236	217	208	218	204
0.5	221	213	205	213	205
0.73	194	194	194	194	194
1.0	177	179	184	179	181
1.5	159	165	171	162	164

TABLE 18.11

Plaice. Natural mortality and growth density dependent; solutions for M and W_∞ at various values of F; mesh constant at 70 mm. (p. 357).

A	B	C
F	M	W_∞ (gm.)
0	0.2000	1,269
0.01	0.1961	1,298
0.05	0.1818	1,417
0.10	0.1670	1,576
0.20	0.1447	1,896
0.30	0.1296	2,184
0.40	0.1190	2,417
0.50	0.1114	2,598
0.73	0.1000	2,867
0.75	0.0993	2,880
1.00	0.0924	3,028
1.50	0.0849	3,168

TABLE 18.12

Haddock. Recruitment and growth density dependent; solutions for R, W_∞ and $t_{p'}$ for various values of F, with mesh constant at 70 mm. (p. 358).

F	A	B	C	D	E	F	G	H	J	K	L	M
	Curve (p) $\left\{\begin{array}{l}\alpha = 0.937 \times 10^{-9} \\ \beta = 3{,}500\end{array}\right\}$			Curve (q) $\left\{\begin{array}{l}\alpha = 0.835 \times 10^{-9} \\ \beta = 5{,}000\end{array}\right\}$			Curve (r) $\left\{\begin{array}{l}\alpha = 0.494 \times 10^{-9} \\ \beta = 10{,}000\end{array}\right\}$			Curve (s) $\left\{\begin{array}{l}\alpha = 0.289 \times 10^{-9} \\ \beta = 13{,}000\end{array}\right\}$		
	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)
0	10.6	760	–	11.9	695	–	19.5	370	–	30.8	110	–
0.10	10.5	846	2.02	11.6	787	2.07	18.5	481	2.48	27.7	163	5.39
0.20	10.4	915	1.97	11.5	862	2.01	18.0	574	2.31	27.0	212	4.02
0.30	10.3	973	1.94	11.3	926	1.97	17.4	660	2.19	26.3	308	3.09
0.40	10.1	1,022	1.92	11.1	981	1.94	16.7	747	2.10	25.1	425	2.61
0.50	9.9	1,063	1.89	10.8	1,029	1.91	15.9	830	2.03	23.4	547	2.35
0.75	9.4	1,144	1.86	9.9	1,126	1.87	12.9	1,019	1.92	17.4	855	2.01
1.00	8.5	1,209	1.83	8.5	1,209	1.83	8.5	1,209	1.83	8.5	1,209	1.83
1.17										0	1,495	1.74
1.33							0	1,495	1.74			
1.50	5.8	1,326	1.79	4.2	1,374	1.78						
1.80				0	1,495	1.74						
2.00	1.1	1,465	1.75									

TABLE 18.13

Haddock. Recruitment and growth density dependent; solutions for R, W_∞ and $t_{p'}$ for various mesh sizes, with F constant at 1.0 (p. 358).

Mesh Size (mm.)	A	B	C	D	E	F	G	H	J	K	L	M
	Curve (p) $\left\{\begin{array}{l}\alpha = 0.937 \times 10^{-9} \\ \beta = 3{,}500\end{array}\right\}$			Curve (q) $\left\{\begin{array}{l}\alpha = 0.835 \times 10^{-9} \\ \beta = 5{,}000\end{array}\right\}$			Curve (r) $\left\{\begin{array}{l}\alpha = 0.494 \times 10^{-9} \\ \beta = 10{,}000\end{array}\right\}$			Curve (s) $\left\{\begin{array}{l}\alpha = 0.289 \times 10^{-9} \\ \beta = 13{,}000\end{array}\right\}$		
	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)	$R \times 10^{-8}$	W_∞ (gm.)	$t_{p'}$ (yrs.)
53.9	6.1	1,370	1.00	4.7	1,395	1.00						
56.5							0	1,495	1.11			
62.0	7.5	1,295	1.39	6.8	1,310	1.39	3.5	1,401	1.37	0	1,495	1.36
70.0	8.5	1,209	1.83	8.5	1,209	1.83	8.5	1,209	1.83	8.5	1,209	1.83
83.0	9.7	1,055	2.76	10.5	1,020	2.79	15.6	790	3.12	–	–	$t_{p'} > t_\lambda$
88.4	10.0	992	3.26	10.9	945	3.33	17.2	600	4.28			
99.0												
100.0	10.3	867	4.80	11.4	790	4.97	–	–	$t_{p'} > t_\lambda$			
120.2	10.5	767	9.13	–	–	$t_{p'} > t_\lambda$						

TABLE 18.14

Plaice. Values of z used to construct the yield curves of Fig. 18.23, and the corresponding transport coefficients referring to the fished area ($_AT$) and the unfished area ($_BT$). (p. 366).

A	B	C	D
% of whole area that is unfished	z	$_AT$	$_BT$
10	9	0.333	3.0
25	3	0.577	1.732
65	0.538	1.364	0.733
80	0.25	2.0	0.5
90	0.111	3.0	0.333

TABLE 19.1

Partition of yield between two fleets, A and B, using constant but different mesh sizes defined by ${}_At_{\rho'} = 3.72$ yrs., ${}_Bt_{\rho'} = 5.0$ yrs. Top entry = yield per recruit to fleet A, $({}_AY_W/R)$; middle entry = yield per recruit to fleet B, $({}_BY_W/R)$; bottom entry = total yield per recruit to both fleets (Y_W/R). Based on plaice. (p. 413).

${}_AF$ / ${}_BF$	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0	0 0 0	215 0 215	257 0 257	252 0 252	237 0 237	221 0 221	209 0 209	197 0 197	189 0 189	182 0 182	176 0 176
0.1	0 223 223	145 126 271	189 76.7 265	198 49.6 248	197 33.7 230	192 23.9 216	187 17.4 205	182 13.1 195	177 10.0 187	173 7.80 181	
0.2	0 287 287	106 174 280	148 113 261	164 76.6 241	170 54.2 225	172 39.6 212	172 29.7 202	170 22.7 192	168 17.6 185		
0.3	0 297 297	82.8 192 275	122 131 253	142 92.4 234	152 67.5 220	158 50.7 208	160 38.7 199	160 30.0 190			
0.4	0 291 291	68.2 198 266	105 140 245	126 102 229	139 76.8 215	146 58.6 205	151 45.5 197				
0.5	0 281 281	58.5 199 258	93.4 145 239	115 109 224	129 83.3 212	138 64.7 202					
0.6	0 271 271	51.7 198 250	84.8 149 233	106 114 220	121 88.2 209						
0.7	0 263 263	46.8 197 244	78.3 151 229	99.6 117 216							
0.8	0 256 256	43.1 196 239	73.2 152 225								
0.9	0 250 250	40.2 194 234									
1.0	0 245 245										

TABLE 19.2

Partition of yield between two fleets exploiting different phases of the life-history of the same population. Fleet A fishing the younger phase between ages $_At_{\rho'} = 2$ yrs. and $_Bt_{\rho'} = 3.72$ yrs. Fleet B fishing the older phase between ages $_Bt_{\rho'} = 3.72$ yrs. and $t_\lambda = 15$ yrs. Second row of table = yield per recruit to fleet A ($_AY_W/R$); in other entries the top figure is the yield per recruit to fleet B ($_BY_W/R$) and the bottom figure the total yield per recruit to both fleets (Y_W/R). Based on plaice. (p. 414).

$_AF$	0	0.01	0.05	0.10	0.20	0.30	0.40	0.50	0.73	1.0	1.5	∞
$_AY_W/R$ $_BF$	0	1.2	5.8	11.2	18.9	26.9	32.7	36.8	44.2	48.7	52.0	37.1
0	0 0	0 1.2	0 5.8	0 11.2	0 18.9	0 26.9	0 32.7	0 36.8	0 44.2	0 48.7	0 52.0	0 37.1
0.01	31.1 31.1	30.5 31.8	28.5 34.3	26.2 37.3	22.0 41.0	18.5 45.5	15.6 48.3	13.2 50.0	8.9 53.0	5.6 54.3	2.4 54.4	0 37.1
0.05	121 121	119 120	111 117	102 113	85.8 105	72.2 99.2	60.8 93.5	51.2 88.1	34.5 78.7	21.7 70.4	9.2 61.2	0 37.1
0.10	181 181	178 179	166 172	152 163	128 147	108 135	90.9 124	76.5 113	51.6 95.7	32.4 81.1	13.7 65.8	0 37.1
0.20	217 217	213 214	199 205	182 194	154 172	129 156	109 142	91.6 128	61.7 106	38.8 87.5	16.4 68.4	0 37.1
0.30	212 212	208 210	195 200	179 190	150 169	127 153	107 139	89.8 127	60.5 105	38.0 86.7	16.1 68.1	0 37.1
0.40	199 199	195 197	183 188	167 179	141 160	119 146	100 133	84.2 121	56.7 101	35.6 84.4	15.1 67.1	0 37.1
0.50	186 186	183 184	171 177	157 168	132 151	111 138	93.6 126	78.8 116	53.0 97.2	33.3 82.1	14.1 66.1	0 37.1
0.73	164 164	161 162	150 156	138 149	116 135	97.7 125	82.3 115	69.3 106	46.7 90.8	29.3 78.1	12.4 64.4	0 37.1
1.00	149 149	146 147	136 142	125 136	105 124	88.7 116	74.7 107	62.9 99.8	42.4 86.6	26.6 75.4	11.3 63.3	0 37.1
1.50	134 134	132 133	123 129	113 124	95.0 114	79.9 107	67.3 100	56.7 93.5	38.2 82.4	24.0 72.7	10.2 62.2	0 37.1
∞	103 103	102 103	95.0 101	87.1 98.3	73.4 92.3	61.7 88.7	52.0 84.7	43.8 80.6	29.5 73.7	18.5 67.3	7.8 59.9	0 37.1

APPENDIX II

LIST OF SYMBOLS AND THEIR DEFINITIONS

It has been necessary, in this paper, to use as symbols nearly all the letters of the English alphabet, capital and small, and the majority of the small letters of the Greek alphabet. Coefficients and parameters referring to important factors have been allotted, wherever possible, a symbol which is retained for that use only. Some duplication has, however, proved unavoidable in order to use symbols appropriate to the factor represented, but in these instances the context is quite different and no ambiguity should arise. The following is an alphabetical list of symbols used for main parameters, together with a brief definition and a section reference to where they are first defined in full or used extensively. The list is not intended to be exhaustive, and does not include symbols used in intermediate stages of algebraic manipulation.

ENGLISH ALPHABET

$A.P.$	Annual Production. Total weight increment produced annually by the post-recruit phase of a fish population; §9.4.3.1.1.
b	Selection factor. Ratio of length of fish at 50% point of a selection ogive (or mean selection length) to mesh size; §§8.1.1.1, 14.2.
a,b	Coefficients of linear equations relating growth to density; §§9.4.2, 16.4.1.
C	Local density of fish. C' = index of local density, in units such as catch per 100 hrs. fishing by a specified ship and gear. A symbol used in dispersion theory; §§10.2.1, 15.1.2.1.
c	Ratio of fishing mortality coefficient to fishing intensity, in equation $F = cf$; §3.3.
D	Dispersion coefficient. Equivalent to mean square velocity in random diffusion theory; §§10.2.1, 15.1.2.1.
d	Average distance covered by a fish in a 'unit movement' ($\equiv$ mean free path); §§10.2.1, 10.2.4.
E	(i) Egg-production. Total number of eggs laid at a spawning season by a fish population; §§6.1.1.1, 6.1.2.
	(ii) Derived parameter referring to anabolism in original form of von Bertalanffy equation; §3.4.
F	Fishing mortality coefficient (instantaneous); §3.3. $\bar{F}$ = effective overall coefficient (in space); §10.2.3.1. F_∞ (in mesh selection theory) = value of F at asymptote of selection curve; §8.1.1.2.
f	Fishing intensity (= fishing effort per unit area); §3.3. $\bar{f}$ = effective overall intensity (in space); §10.2.3.1. f' = effective constant intensity (in time); §14.1.1.2. $\bar{f}'$ = combination of $\bar{f}$ and f'; §14.1.1.4.
G	Grazing mortality coefficient, generated by a fish population in a food species; §9.4.3.2.3.

g (i) Grazing mortality coefficient generated by an individual fish; §9.4.3.2.3.
(ii) Fishing effort ($=$ total fishing time per year) in §5.1 only.

H Coefficient of synthesis in differential form of von Bertalanffy equation (3.4); §3.4.

I Index of fishing intensity. Fishing intensity as a ratio of pre-war intensity; §20.2.1.

j Exponent in (9.16), viz. $d\xi_A/dt = \zeta w^j$, expressing maintenance requirements of an individual fish as a function of its body weight; §9.4.3.1.1.

K (i) One of the two main parameters of the von Bertalanffy growth equation. Equal to 1/3 of the catabolic coefficient k; §3.4.
(ii) Constant relating true local density to index of density (e.g. catch per 100 hrs. fishing); §15.1.2.1.

k (i) Coefficient of catabolism in differential form of the von Bertalanffy growth equation (3.4); §3.4.
(ii) $1/k =$ maximum possible rate of assimilation of net energy by an individual fish, in Kostitzin's equation (9.26); §9.4.3.1.2.
(iii) $k_1, k_2 =$ coefficients defining fishing mortality coefficient F as a linear function of age t; §§8.1.1.2, 8.1.2.

L (i) Length of individual fish (particular).
$L_\rho =$ length at recruitment; §18.4.1.
$L_{\rho'} =$ length at entry to exploited phase ($\equiv$ mean selection length); §8.1.1.1.
$L_\infty =$ asymptote of curve of growth in length; §3.4.
$\bar{L}_Y =$ mean length of fish in catch or exploited phase, §5.4.
(ii) Coefficient of detachment of marks from living fish; §14.1.2.3.

l Length of individual fish (general). E.g. in growth equations $l_t =$ length at age t; §3.4.

M Natural mortality coefficient (instantaneous); §3.2.
$\underline{M} =$ equivalent constant natural mortality coefficient; §7.3.2.

m Apparent mortality coefficient; §15.1.2.2.
m_0, $m_1 =$ coefficients defining natural mortality rate as a linear function of age; §§7.2.1, 14.3.1.

N Number of fish in a homogeneous group.
$\bar{N}_X =$ mean number of fish present in year X; §13.1.
$N_t =$ number at age t; §4.1.
$N_0 =$ number in batch of marked fish liberated at time zero; §14.1.1.1.

n Number of marked fish recaptured in a given period, e.g. n_1 in first recapture period, etc.; §14.1.1.1.

P Population size.
$\bar{P}_W =$ annual mean biomass of post-recruit phase; §5.3.
$\bar{P}_W =$ annual mean biomass of exploited phase (approximately proportional to catch per unit effort); §5.3.
${}_\eta\bar{P}_W =$ annual mean biomass of mature phase; §6.1.2.
$\bar{P}_N, \bar{P}'_N =$ annual mean numbers in post-recruit and exploited phases respectively; §5.2.

p As a prefix, denotes a predicted characteristic. E.g. $({}_pS^2_Y)_q =$ predicted variance of yield measured over q years; §15.2.2.
$\bar{p}_W =$ standing crop (weight) of food population; §9.4.3.2.3.
$p_\theta =$ proportion of females of age-group θ that are mature; §6.1.2.

Q Maintenance energy coefficient. Product of maintenance food coefficient ζ and efficiency of utilisation coefficient ε ; §9.4.3.1.2.

q (i) Weight-length coefficient, in equation $w = ql^3$; §§3.4, 16.1.
(ii) As a prefix or suffix to denote number of years over which an average yield, $_{q}\bar{Y}_{W}$, variance of yield $(S^2_Y)_q$, etc. is measured; §§6.2, 15.2.2.

R Number of fish recruited annually to exploited area at age t_ρ; §3.1.
R' = number entering exploited phase each year at age $t_{\rho'}$; §3.1.

r (i) Annual recruitment to a food population; §9.4.3.2.3.
(ii) Successive recapture periods in analysis of marking experiments; §14.1.1.1.

S (i) Observed standard deviation. S_Y = of annual yield, S_R of recruitment; §§6.2, 15.2.2.
(ii) Grazing efficiency; e.g. $_{A}S_{B}$ = grazing efficiency on food B relative to food A; §9.4.3.2.4.

s (i) Sex-ratio. Percentage of mature females in total mature population; §6.1.2.
(ii) Current speed; §10.2.5.
(iii) Physiological surface area in differential form of von Bertalanffy equation (3.4); §3.4.

T (i) Transport coefficient, defining rate of interchange of fish between adjacent areas; §§10.2.1, 14.1.2.4.
(ii) $\bar{T}_Y$ = mean age of fish in catch or exploited phase; §5.5.

t Age of fish.
t_ρ = age at recruitment; §3.1.
$t_{\rho'}$ = age at entry to exploited phase ($\equiv$ mean selection age); §§3.1, 8.1.1.4.
t_λ = maximum age; §3.2.
t_0 = arbitrary origin of growth curve; §3.4.
t_η = age at first maturity; §6.1.2.

U Sum of squares of residuals; §14.3.2.2.

u u_θ = yield per recruit contributed by fish of age-group θ ; §15.2.2.
$_{x}u$ = ratio of grazing mortality coefficients in two steady-states; §9.4.3.2.3.

u,v Co-ordinates defining sub-areas in transport equations; §10.2.2.

V Effective velocity of movement of fish; §10.2.1.
V' = true swimming speed; §10.2.4.
V_r = resultant velocity (relative to bottom); §10.2.5.

W Weight of individual fish (particular).
W_ρ = weight at recruitment; §9.2.1.
$W_{\rho'}$ = weight at entry to exploited phase ($\equiv$ mean selection weight); §9.2.1.
W_∞ = asymptote of curve of growth in weight; §3.4.
$W_{\infty L}$ = limiting value of W_∞ when food is unlimited; §9.4.3.2.2.
$W_{\infty M}$ = maximum possible value (theoretical) of W_∞; §9.4.3.1.2.
$\bar{W}_Y$ = mean weight of fish in catch or exploited phase; §5.4.
W_η = weight at first maturity; §6.1.2.

w Weight of individual fish (general).
w_t = weight at age t, in growth equations; §3.4.

X (i) Denotes a particular year, usually as a suffix.
F_X = fishing mortality coefficient in year X; §8.2.1.
${}_XY_W$ = yield in year X; §8.2.1.
${}_\theta\bar{N}_X$ = mean abundance of age-group θ in year X; §14.3.1.
(ii) 'Other-loss' coefficient in marking theory; §14.1.1.1.

Y Yield.
Y_W = annual yield in weight; §4.1.
Y_N = annual yield in numbers; §4.2.

z Ratio of fished to unfished areas, in dispersion theory; §10.2.2.

GREEK ALPHABET

LETTER	NAME	
α	alpha	Derived coefficients of pre-recruit mortality, relating recruitment to egg-production in (6.10); §§6.1.1.1, 15.2.3.
β	beta	
Γ	Gamma	Index of competition between two fish populations grazing the same food population; §11.2.1.
γ	gamma	Egg-production per recruit, $E = \gamma R$; §6.1.1.1. Note: (i) α, β and γ are used in transport equations to denote certain combinations of F, M, T and nK; §10.2.2. (ii) α, β, γ and δ are used in transitional yield equations to denote certain combinations of F, M and nK; §8.2.2.
Δ	Delta	Finite difference symbol. In discontinuous approximation to a selection ogive; §8.1.1.3. Also in analysis of food and growth data; §16.4.2.
ε	epsilon	Coefficient of utilisation of food for growth and maintenance; §9.4.3.1.1. ε_0 = maximum value of ε; §9.4.3.1.2.
ζ	zeta	Maintenance food coefficient; §9.4.3.1.1.
η	eta	Suffix denoting reference to spawning or maturity. t_η = age at first maturity, W_η = weight at first maturity, τ_η = date of spawning, $N^{♀}_{\tau_\eta}$ = number of mature females present on date of spawning; §6.1.2.
θ	theta	Age-group number. ${}_\theta\bar{N}_X$ = number of fish of age-group θ in year X; §14.3.1. θ_ρ = youngest age-group into which recruitment occurs; §16.3.1. $\bar{w}_{\theta_\rho}$ = mean weight of fish of age-group θ_ρ; §16.3.1. u_θ = yield per recruit obtained from fish of age-group θ; §15.2.2.
$\varkappa$	kappa	Constant relating fishing mortality coefficient to 'destruction' mortality in food organisms caused by fishing gear; §9.4.3.4.
λ	lambda	Fishable life-span ($= t_\lambda - t_{\rho'}$); §4.1. λ' = 'grazeable' life-span of food organisms; §9.4.3.2.3.
μ	mu	μ_1, μ_2 = coefficients relating natural mortality rate to density, e.g. in (6.8) and (7.7); §§6.1.1.1, 7.3.

ν	nu	Nutritional factor; §9.4.3.1.2. $1/_A\nu_B$ = number of gms. of food B required to produce same rate of growth as 1 gm. of food A; §9.4.3.2.4.
Ξ	Xi	Annual food consumption of a fish population. Ξ_A = maintenance food consumption; §9.4.3.1.1. Ξ_B = growth food consumption; §9.4.3.1.1. Ξ_L = limiting food consumption, i.e. practical limit to annual food consumption of a population (see $W_{\infty L}$); §9.4.3.2.2. Ξ' = gross energy consumption; §9.4.3.2.4.
ξ	xi	As for Ξ, but referring to an individual fish.
ρ	rho	Duration of pre-exploited phase ($\rho = t_{\rho'} - t_\rho$); §4.1, (see diagram, p. 28).
$\sum$	Sigma	Summation sign. E.g. in growth equations, §3.4; in control chart theory, §19.2.3.
σ	sigma	(i) Theoretical standard deviation. σ_R, of recruitment, σ_Y, of annual yield; §§6.2, 15.2.2. (ii) In Kostitzin's equation (9.26), = maximum efficiency of utilisation of food ($\equiv \varepsilon_0$); §9.4.3.1.2.
τ	tau	(i) Calendar date. τ_η = date of spawning; §6.1.2. $\tau_{\rho'}$ = date at which an age-group enters exploited phase; §8.2.2. (ii) Recapture period (in marking theory). Period of time over which recaptures of marked fish are summed; §14.1.1.1.
Φ	Phi	Total number of age-groups into which recruitment occurs, i.e. number of recruit sub-groups; §§6.1.4, 9.3.
ϕ	phi	(i) A 'dummy' time variable. E.g. N_ϕ = number of fish present after fraction ϕ of a year has elapsed; §§4.2, 8.2.1. See also ψ. (ii) A general function. E.g. $\phi'(F)$ = running costs as a general function of F; §19.1.3.
χ	chi	Fecundity coefficient. Number of eggs laid per gm. weight of mature females in a spawning season; §6.1.2.
ψ	psi	Used mainly as a 'dummy' time variable. E.g. in linear approximation to a selection ogive; §8.1.1.2.
Ω	Omega	Summation constant in von Bertalanffy equation for growth in weight (3.9); §3.4.
ω	omega	Average weight of individual food organisms during their 'grazeable' life-span; §9.4.3.2.3.

APPENDIX III

Derivation of indices of total European fishing effort on North Sea plaice and haddock during the pre-war period (Table 14.15, §14.3.2.2.)

PLAICE

Table I gives the derivation of average power factors of motor and sailing trawlers and steam and motor seiners, in terms of steam trawlers. The power factors for motor and sailing trawlers (cols. D and E) have been obtained by comparing their average catches of plaice per 100 hours fishing (cols. B and C) with that of steam trawlers (col. A) fishing in region IVc, since nearly all the motor and sailing trawler effort was expended in this region. For a similar reason, the power factors of steam and motor seiners (cols. J and K) have been obtained by comparison with steam trawlers (col. F) fishing in region IVb. The origins of the data of Table I are as follows:

Columns A and F: Sea Fisheries Statistical Tables (Table 10)
Columns B, C, G and H: ,, ,, ,, (Table 6)

Table II gives the annual fishing effort of the various types of vessels mentioned above (cols. A-E) and the standardised efforts (cols. F-J) using the power factors derived in Table I. The fishing effort is that in regions IVb and IVc, which together cover the main part of the plaice population. All the effort data refer to English vessels only and are in the units hours fishing $\times 10^{-6}$; they are obtained from Table 4 of the Sea Fisheries Statistical Tables.* Cols. F, G, H and J of this table are the products of cols. D, E, J and K of Table I and cols. B, C, D and E of Table II respectively, and hence give the fishing effort by the various types of vessels in steam trawler units. These are totalled in col. K to give indices of total English fishing effort. To obtain indices of total European fishing effort on plaice (col. M), the English indices of col. K are raised by the ratio of the total European catch of North Sea plaice in each year to the English catch, given in col. L (Bulletin Statistique).†

HADDOCK

The English fleet fishing North Sea haddock consisted mainly of steam trawlers but included some steam and motor seiners. The fishing effort of motor trawlers was largely confined to region IVc and need not therefore be considered in the case of haddock, since this fish is found mainly in the central and northern regions of the North Sea.

Table III gives the derivation of power factors relating to haddock of steam and motor seiners (cols. D and E) in terms of steam trawlers. Data of catch per 100 hours fishing by seiners are not available for regions IVa and IVb separately, but since their activity was restricted mainly to regions IVa and IVb it is sufficient to compare their catches of haddock per 100 hours fishing with those of steam trawlers for these regions only (Sea Fisheries Statistical Tables, Tables 4 and 6).

Raitt (1939, Table 5) gives the total English and Scottish steam trawling effort in the whole of region IV, but this includes English fishing in region IVc which was not on haddock. Subtracting the latter therefore gives estimates of the total hours fishing by English and Scottish first class steam trawlers in regions IVa and IVb; this is shown in col. A of Table IV. The adoption of the Vigneron-Dahl gear occurred progressively over

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*Published by H.M.S.O. London.
†Published by I.C.E.S. Copenhagen.

the period 1923-1926. We have assumed that in 1924 one-half of the trawler fleet was using V.D. gear, three-quarters in 1925, and that from 1926 onwards the modified gear was in universal use. The corrected figures of British steam trawler effort in regions IVa and IVb, using Raitt's factor of 1.42 for the increased fishing power of V.D. gear, are given in col. B of Table IV.

The hours fishing in these regions by English steam and motor seiners are given in cols. C and D; the corresponding fishing efforts in steam trawler units are given in cols. E and F. The latter are the products of cols. D and E of Table III and cols. C and D of Table IV respectively. Indices of total British fishing effort on haddock are given in col. G, obtained by summing cols. B, E and F. Finally, these are raised by the ratios of the European to British catch of North Sea haddock given in col. H (Bulletin Statistique) to give the indices of total European fishing effort in col. J.

TABLE I

Plaice: estimates of fishing power of steam and motor seiners in terms of steam trawler fishing power

	A	B	C	D	E	F	G	H	I	K
Year	Catch of plaice in cwts. per 100 hrs. fishing by English 1st class trawlers Region IV C					Catch of plaice in cwts. per 100 hrs. fishing by English 1st class seiners and steam trawlers Region IV B				
	Steam	Motor	Sail	Motor / Steam	Sail / Steam	Steam trawlers	Steam seiners	Motor seiners	Steam seiners / Steam trawlers	Motor seiners / Steam trawlers
1929	33	19	11,0	0,58	0,33	16	25	72	1,56	4,50
1930	29	13	9,5	0,45	0,33	15	20	71	1,33	4,73
1931	28	15	8,5	0,54	0,30	15	22	82	1,47	5,47
1932	27	13	7,8	0,48	0,29	15	25	47	1,67	3,13
1933	31	13	7,7	0,42	0,25	15	9	28	0,60	1,87
1934	30	14	7,5	0,47	0,25	15	10	28	0,67	1,87
1935	31	11	7,3	0,35	0,24	15	7	25	0,47	1,67
1936	32	16	9,6	0,50	0,30	17	8	20	0,47	1,18
1937	31	15	9,4	0,48	0,30	17	6	22	0,35	1,29
1938	29	12	8,4	0,41	0,29	18	15	25	0,83	1,39

TABLE II

Plaice: estimates of European fishing effort indices, in British steam trawler units.

Year	A	B	C	D	E	F	G	H	J	K	L	M
	Fishing by English 1st class vessels in hrs. × 10^{-6}—Regions IVb and IVc					Corrected hrs. fishing × 10^{-6} in steam trawler units				English fishing effort index	Ratio of European to English catch of plaice	European fishing effort index
	Steam trawlers	Motor trawlers	Sailing trawlers	Steam seiners	Motor seiners	Motor trawlers	Sailing trawlers	Steam seiners	Motor seiners			
1929	1.614	0.011	0.376	0.059	0.006	0.006	0.124	0.092	0.027	1.86	3.12	5.81
1930	1.634	0.020	0.324	0.063	0.006	0.009	0.107	0.084	0.028	1.86	3.14	5.84
1931	1.512	0.035	0.280	0.043	0.009	0.019	0.084	0.063	0.049	1.73	2.87	4.97
1932	1.388	0.051	0.246	0.042	0.010	0.024	0.071	0.070	0.031	1.58	3.11	4.91
1933	1.602	0.057	0.216	0.046	0.017	0.024	0.054	0.028	0.032	1.74	2.98	5.19
1934	1.644	0.059	0.175	0.044	0.019	0.028	0.044	0.029	0.036	1.78	2.78	4.94
1935	1.526	0.065	0.114	0.034	0.023	0.023	0.027	0.016	0.038	1.63	2.84	4.63
1936	1.481	0.070	0.071	0.029	0.021	0.035	0.021	0.014	0.025	1.58	2.81	4.44
1937	1.381	0.087	0.052	0.018	0.027	0.042	0.016	0.006	0.035	1.48	2.96	4.39
1938	1.132	0.097	0.033	0.021	0.019	0.038	0.009	0.018	0.028	1.23	3.49	4.30

TABLE III

Haddock: estimates of fishing power of steam and motor seiners in terms of steam trawler fishing power.

	A	B	C	D	E
Year	Catch of haddock in cwts. per 100 hrs. fishing by English 1st class vessels				
	Steam trawlers IVa and IVb	Steam seiners IV	Motor seiners IV	$\frac{\text{Steam seiner}}{\text{Steam trawler}}$	$\frac{\text{Motor seiner}}{\text{Steam trawler}}$
1924	48	59	30	1.23	0.62
1925	82	79	26	0.96	0.32
1926	81	76	21	0.94	0.26
1927	60	60	11	1.00	0.18
1928	60	63	9	1.05	0.15
1929	56	89	11	1.59	0.20
1930	69	109	18	1.58	0.26
1931	56	98	18	1.75	0.32
1932	53	82	10	1.55	0.19
1933	51	129	36	2.53	0.71
1934	33	66	13	2.00	0.39
1935	24	48	17	2.00	0.71
1936	20	36	8	1.80	0.40
1937	24	77	27	3.21	1.12
1938	25	48	19	1.92	0.76

TABLE IV

Haddock: estimates of European fishing effort indices, in British steam trawler units.

Year	A	B	C	D	E	F	G	H	J
	Fishing by British vessels in IVa and IVb (hrs. × 10)$^{-6}$				Corrected hrs. fishing × 10^{-6} in steam trawler units		British fishing effort index	Ratio of European to British catch of haddock	European fishing effort index
	Steam trawlers	Corrected for V.D. gear	Steam seiners	Motor seiners	Steam seiners	Motor seiners			
1924	2.348	2.001	0.339	0.009	0.417	0.006	2.424	1.27	3.08
1925	2.349	2.175	0.246	0.007	0.236	0.002	2.413	1.24	2.99
1926	1.959	1.959	0.190	0.009	0.178	0.002	2.140	1.26	2.70
1927	2.309	2.309	0.149	0.006	0.149	0.001	2.459	1.30	3.19
1928	2.266	2.266	0.086	0.006	0.090	0.001	2.357	1.25	2.93
1929	2.283	2.283	0.059	0.006	0.094	0.001	2.378	1.23	2.94
1930	2.273	2.273	0.062	0.005	0.098	0.001	2.372	1.26	2.98
1931	2.001	2.001	0.044	0.008	0.076	0.003	2.080	1.30	2.70
1932	1.929	1.929	0.043	0.010	0.066	0.002	1.997	1.25	2.49
1933	2.216	2.216	0.046	0.016	0.116	0.012	2.344	1.23	2.88
1934	2.277	2.277	0.045	0.020	0.090	0.008	2.375	1.28	3.03
1935	2.275	2.275	0.034	0.022	0.069	0.016	2.360	1.28	3.03
1936	2.134	2.134	0.029	0.022	0.052	0.009	2.195	1.30	2.86
1937	1.882	1.882	0.018	0.028	0.058	0.031	1.971	1.28	2.53
1938	1.729	1.729	0.021	0.020	0.040	0.015	1.784	1.28	2.29

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